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THE PRINCIPLES OF PSYCHOPHYSIOLOGY

By

L. T. TROLAND

IN FOUR VOLUMES

I. The Problems of Psychology; and Perception
II. Sensation
III. Cerebration and Action
IV. The Ultimate Theory of Mind and Matter

The Principles of
Psychophysiology

A Survey of Modern Scientific Psychology

By

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Assistant Professor of Psychology, Harvard University; Author of "The Fundamentals of Human Motivation," "The Mystery of Mind," "The Nature of Matter and Electricity," etc.

WITH ORIGINAL DRAWINGS BY THE AUTHOR

VOLUME II

SENSATION

WITHDRAWN

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PREFACE TO VOLUME TWO

The general and specific purposes of the present work have been discussed in detail in the preface to the first volume, to which the reader is referred for a complete exposition of points of view and methods. The first volume deals with three problems: (1) the definition or nature of psychological knowledge, (2) the tasks and methods of psychophysiology and (3) perception. The second volume, here offered, is devoted entirely to the problem of *sensation.* Although a complete appreciation of the treatment of this subject may demand conversancy with the contents of Volume I, an attempt has been made to present the facts in such a manner as to make the discussion usable as a text on sensation, by itself. To this end, the present volume begins with a detailed analysis of the concept of sensation, followed by a formulation of the special interpretation of this concept which is demanded by the general method of the whole work.

By way of further elucidation, a few words may be devoted to a summary of the general method in question. Psychology is defined as the science which describes consciousness (or immediate experience) and its manner of determination by factors lying outside of itself. Such factors appear to be restricted to the world of physical science, and to be grouped about the activities of living organisms. For each individual experience system, there is a corresponding *response* system. An analysis of response systems shows that they comprise complex mechanisms for the conduction or propagation of an influence from one part of space to another, along a definite conductional path. This path begins in the vicinity of a sense-organ (such as the eye) and ends in the zone of effectiveness of muscular or effector organs. The connecting linkage consists of the afferent, central and efferent nervous systems. We have conceived response to embrace, not only the mechanisms and processes which are within the organism, but also those environmental factors which are causally continuous with the intraorganic changes.

Psychophysiology is the science which endeavors to ascertain the laws that link consciousness or immediate experience with the variables and phases of response. Since the latter is a propagational sequence of events which are more or less distinct from one another, it is convenient to consider the relationship between consciousness and various such response "stages," separately. We have good reason for believing that the "direct determination" of consciousness rests in activities occurring in a restricted region of the cerebral cortex, a very small section of the total conduction path. However, our knowledge of these direct relationships has been relatively little developed compared with that of indirect relationships, such as those between consciousness and the objective world or between consciousness and behavior. We have defined "perception" so that it is concerned with the former of the just mentioned relations, and have presented the facts in some detail in Volume I. The present volume, dealing with sensation, is concerned with the indirect relationships between consciousness and the so-called "afferent arc," or the sector of the nerve conduction path which starts with the sense-organ stimulus and ends at the sensory projection areas of the cerebral cortex.

L. T. TROLAND

CAMBRIDGE, MASS.,
MARCH, 1930.

GENERAL PREFACE

The present work is an exposition of the facts and principles of psychology in accordance with a definite method. This is, in general, *the method of psychophysiology*. In greater detail, the treatment is based upon an analysis of the process of neuromuscular response, together with the familiar postulate that consciousness is correlated with, but distinct from, the *cerebral* factor in these physiological operations. The scheme is thus that of traditional "physiological psychology," brought up to date, but I believe that its refinement and modernization may prove to be as important as is its historical core. Small changes in point of view may reveal new aspects of the system of psychology as a whole, enabling one to straighten out some very ancient tangles in a quite satisfactory manner.

My aim in preparing this work has been rather complex. Aside from irrelevant personal motives, the main purposes which I have had in mind may be summarized as follows. Firstly, to examine the foundations of psychology as a science, in order to arrive at a satisfactory statement of its problems and methods. Secondly, to formulate a plan for treating these problems and facts which would thrust aside nothing that is of real human importance. Thirdly, to present, in accordance with this plan, what seem to me to be the most important facts and theories of psychological science. Fourthly, to reconsider the question of the mind-body relationship from the philosophical standpoint. Finally, to formulate certain philosophical developments of all of these studies.

In connection with my first purpose I have been stimulated by a desire to refute the position which is taken by the modern behaviorists in psychology, and yet to preserve what is valuable in behavioristic practice. In a sense, this work in its entirety is presented as a detailed, demonstrative, reply to the behavioristic contention that the introspective method in psychology is worthless. However, I have not rejected, but have, rather, adopted the behavioristic methods insofar as they are positive. I have insisted upon viewing the organism as a physical machine, the operations of which can be described without reference to consciousness. Nevertheless, this very reference creates the principal purpose and problem of the book. I shall be greatly interested to know what objections the behavioristic psychologists can raise against the arguments and analyses which I have offered, and I shall be surprised if there are any introspective psychologists who disagree seriously with the general system which is developed in this book.

It is therefore my hope that the work may accomplish something towards effecting a reconciliation between the behavioristic and the introspectionistic schools, and may thus aid in unifying the progress of psychological science. The present controversial situation certainly constitutes an undesirable distraction from the many important problems which are pressing upon psychology for solution. Also, because of the apparent deadlock which exists between the opposing schools, psychology is losing the respect both of the scientific world and of the public. This is occurring at a time which is, in general, quite favorable for an increase in such respect. The world to-day has a greater interest in philosophical and psychological problems than it has ever had before. People are beginning to realize that these fields of study should be capable of supplying information which may be of the greatest possible value in regulating the conduct of life.

The second of my purposes is concerned with the details of the psychophysiological method. This method recognizes the existence of consciousness as a distinctive psychical entity, which cannot be reduced in any sense to terms of physics or of physiology. However, consciousness, as I have conceived it, is a very concrete and real thing, nothing less than a section of experience itself. I have assumed, with the classical physiological psychologists, that the individual consciousness is correlated with processes occurring in certain areas of the cerebral cortex. Such processes are, of course, stages or links in a chain of neuromuscular events, all of which must be conceived ultimately in physical terms. This chain of events takes the form of a physical propagation, starting in the environment, and being transmitted along neural channels until it finally reaches the environment again. I have considered the task of psychophysiology to be that of determining the relationships which hold between consciousness and various segments of this propagational series.

The natural subdivisions of the response propagation furnish the cue for a classification of such psychophysiological relationships. Under the caption of *perception,* I have discussed those relationships which obtain between consciousness and the world outside of the organism, at the beginning of the propagational series of events. I have taken the term, *sensation,* to stand for the relationship between consciousness and processes in the afferent nervous arc, including the sense-organs and their immediate stimuli. Under the heading of *cerebration,* I have considered the direct psychophysical relationship between consciousness and brain activity, as well as indirect relationships with other central processes. I have taken the word, *action,* to stand for psychophysical relations which hold between consciousness and events on the efferent, or outgoing, sector of the response path. It is true that these applications of the terms, perception, sensation, cerebration and action, involve some redefinitions, but I believe that the changes in meaning which I have introduced are scientifically advisable.

When we come to the third of my expressed purposes, I may expect to encounter some adverse criticism of its presented realization. It is impossible in any book of practicable size to set forth all of the facts of psychophysiology. It would be even more difficult to expound all of the theories which have been offered in this field of thought. Hence I have been compelled to select those facts and theories which seem to me to be the most important, and I have necessarily chosen these from my own stock of information. Doubtless there are some regrettable omissions, but it has been my endeavor to prepare a reasonably comprehensive and detailed treatment of the facts. I shall be indebted to anyone who may care to communicate to me criticisms which may have a bearing upon the contents of possible later editions of this work.

Some may feel that I have been particularly presumptuous in my treatment of theories. Here I have followed the suggestion of my colleague, Dr. Beebe-Center, and have neglected to consider what he designates as "duds," or doctrines which are definitely out of date and in clear disagreement with established facts. This procedure is quite contrary to the conventional practice in textbooks of psychology. It is customary to present a long list of alternative hypotheses. The danger comes, of course, in attempting to distinguish between the "duds" and the live ideas, in particular instances. The writer himself must take the chances which are involved in making such decisions. I have contented myself, as a rule, with formulating a single theoretical interpretation of the facts which seems to me, in the given situation, to be the most satisfactory one in the present state of our enlightenment, and I have done this without much reference to the historical sources of the theory in question. Those who are interested in a review of classical guesses are referred to other textbooks, or to historical treatises.

I have divided the treatment of the facts and theories of psychophysiology under the four headings of Perception, Sensation, Cerebration and Action, each of which corresponds to a unit Part of the present work.

Under the influence of the fourth of my expressed purposes, I fear that my presumption has reached extreme limits, for here I have dared to suggest a scientific basis for what passes as philosophy. In the time of the Greeks, the word philosophy stood for all knowledge. Gradually, one by one, the definite sciences have emerged from its womb, but certain forms of inquiry still remain in an embryonic condition. The principal ones are known as epistemology, ontology (or cosmology) and ethics. I believe that these disciplines, also, can be made scientific; but, in order that this may be accomplished, their status must undergo a shocking transition, which cannot fail to bring pain to academic philosophy. (However, these pains may be the agonies of parturition.) It is necessary, according to my view, to regard epistemology, cosmology and ethics as *developments from the facts of psychophysiology.*

To an unbiased thinker, this thesis will not appear unreasonable. Knowledge is surely a mental function, and knowledge of the physical world must be regarded as a psychophysical relationship. Knowledge of a *metaphysical* world may conceivably involve some fundamentally new terms, but it is my contention that, in fact, the latter are basically those of introspective psychology and of physical theory. The key to a cosmological inquiry into the nature of "things in themselves" is to be found in the psychophysical relations which are demonstrated by psychophysiology. Ethics should be interpreted as a practical development of human motivational and of cosmological principles. I have endeavored to present these ideas in definite form in the fourth volume, and to provide schematic developments for the disciplines in question.

In concluding my general comments, I may be permitted to say that I have presented in this book what seems to me to be the living substance of modern psychology. Psychophysiology is something more than a special way of viewing psychological facts. It is the essence of what we have learned that is valuable in the domain of psychological inquiry. I stoutly maintain that the behaviorist's view of the science is a fearful error. I assert, with equal firmness, that a psychology by pure introspection is possible and necessary. But I do not believe that a purely introspective psychology can be made *valuable* unless it is correlated with the facts which the behaviorists are emphasizing. Either extreme in method yields a result which is not only less than the facts, but something which, by itself, is practically worthless. Strict behaviorism and strict introspectionism are, indeed, artificial academic creations. The living and growing truths of psychology are psychophysiological. Both behaviorists and pure introspectionists unwittingly contribute to the development of this science, but their accomplishments for posterity would be increased if they would envisage all of the facts with a clear and open mind.

Something should probably be said here concerning the relation of my treatment of psychology in the present work to the modern controversy between the *Gestalt* (or configurational) and the structural schools of psychology. I confess that the arguments of the configurationists and the methods of the Titchenerian structuralists both appeal to me very strongly. As in the behavioristic debate, I consider that the positive contentions on both sides of the argument are generally correct. The problem before the constructive thinker is to eliminate the negative propositions and to arrive at a satisfactory compromise which will permit the theory to check with the facts. A sympathetic and tolerant *Gestalter* will, perhaps, consider the present book a contribution to his own movement. I shall not be at all displeased at such a reaction. On the other hand, I believe that Professor Titchener, himself, if he were still alive to read this work, would not be offended by its methods.

The following comments may be made regarding the physical make-up of this work. It is essentially a continuous treatment of psychophysiological problems, but it has been divided into four volumes in the hope of increasing its general usefulness. Some readers will not be interested in the more philosophical discussion. Other readers may be concerned primarily with the higher mental processes, still others with sensation, and there may be some who are interested only in the foundations of psychology.

The first volume embraces the first three Parts, dealing with the definition of psychology, with the methods of psychophysiology and with perception, respectively. The inclusion of perception in this volume is due primarily to the desirability of a reasonably even subdivision of pages. However, it has the advantage of offering a concrete example of the psychophysiological method, which is pursued throughout the work, to those who may not care to read the volumes on sensation and on cerebration and action. Perception deals with the common sense facts of psychophysiology, while the later Parts are concerned with more subtle and esoteric matters.

The second volume provides a unified treatment of sensation, as I have defined this concept above. Action and cerebration are discussed in the third volume, and fall together quite naturally. The fourth volume is devoted wholly to the philosophical developments of psychophysiological facts and principles: an analysis of the ultimate significance of the mind-body relationship, and an attempt to found a new philosophical methodology.

For the benefit of those who may wish to use the later volumes without consulting earlier ones, summaries of essential points in the argument of the book as a whole are presented at the beginning of each volume. Essential matters of detail are repeated in fine print at appropriate places in successive volumes or are dealt with in footnotes.

I wish to acknowledge my indebtedness to the following persons for the assistance which they have given me in the preparation of this work: Dr. J. G. Beebe-Center, for a preliminary reading of the manuscript, numerous helpful suggestions, and in particular for many references in the literature on the topic of affection; Mr. A. D. Fuller, Jr.; Dr. T. F. Karwoski and Mr. Eugene F. McCarthy for assistance with the proof; and to Dr. Karwoski and my wife for help in preparing the reference lists, the index and other details of the manuscript.

L. T. TROLAND

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CONTENTS

PAGE
Preface to Volume Two iii
List of Illustrations xix

PART FOUR

SENSATION: CONSCIOUSNESS AND THE AFFERENT ARC

CHAPTER PAGE
XIII. The Concept of Sensation 1

Section 50 — The General Nature of Sensation: Current Definitions of Sensation. Sensory Psychophysiology, and Analysis. Various Further Aspects of Sensation. *Section 51 — The Analysis of the Afferent Arc:* The General Nature of the Stimulus. The Sense-Organ Process. The Receptor Process. The Nerve Excitation and Conduction. The Various Departments of Sensation. *Section 52 — The Physical Nature of the Nerve Process:* The Present Status of Nerve Physiology. Methods of Thought Concerning Nerve Physiology. The Resting State of the Nerve Cell. The Mechanism of Excitation. The Mechanisms of the Threshold and of Propagation. Special Evidences of Increased Permeability During Excitation. Resistance of the Nerve Cell to Excitation. The Basis of du Bois-Reymond's Law and of Electrotonic Effects. Refractory Phase and Allied Conditions. The Energetics of Nerve Action. The All-or-None Principle. Temporal Characteristics of Individual Nerves; Chronaxy. The Basis of Nerve Current Strength. The Mechanism of Receptor Cells. An Example of Receptor Action. The Special Properties of Synapses. Special Processes at Synapses.

XIV. Visual Sensation 51

General Analysis of the Problem. The Principal Aspects of Color Sensation. The Problem of Binocular Sensation. *Section 53 — The Nature of the Visual Stimulus:* Light and Radiant Energy. The Three Characteristics of Radiant Energy. Measures of Wave-Length. Radiometric and Photometric Intensity Measures. Distribution Curves of Common Radiant Sources. Aspects of Reflection and Transmission. *Section 54 — Monocular Stimulus Relationships Involving Brilliance: I. Brilliance as a Function of Wave-Length:* The Direct Psychophysical Function. Visibility Curves. The Purkinje and Allied Phenomena. Light as a Psychophysical Concept. Methods of Heterochromatic Photometry. *II. Brilliance as a Function of Intensity:* The "Absolute Threshold." Supraliminal Brilliance as a Function of Intensity. Brilliance and Wave-Length Composition. *III. Brilliance as a Function of Spatial Factors:* Field Functions. Pattern Functions Involving Area. Pattern Functions; Contrast. *IV. Functions Which Determine Brilliance Patterns:* Acuity as a Function of Stimulus Intensity. Irradiation.

CHAPTER PAGE

V. Brilliance as a Function of Time: The Time Threshold. The Growth Curve for Brilliance. The Decay Curve and Charpentier's Bands. Positive After-Images. Brilliance Flicker and Fusion. Photopic Brilliance Adaptation. (Negative After-Images. Achromatic Dimming Effects.) Scotopic Adaptation. *Section 55 — Monocular Refractive Relations of Brilliance:* The Gross Anatomy of the Eyeball. (The Dioptric Parts. The Pupil. The Optic Nerve.) The Minute Structure of the Retina. (The Structure of the Rod and Cone Cells. Local Differences in Retinal Structure.) Some Fundamental Conceptions in the Optics of the Eye. Further Intraocular Effects. Entoptic Factors in Sensory Relationships. Brilliance-Wave-Length Functions. Brilliance-Intensity Relationships. (Retinal Illumination. Absolute Thresholds. The Fechner Function.) Effects of Scattered Light. Refractive Distortions. "Entoptic Phenomena." Field Functions. Pattern Functions. Acuity. Temporal Functions. *Section 56 — Monocular Neurological Relations of Brilliance:* The Problem of Visual Theory. The Duplexity Theory. Facts Explained by the Duplexity Theory. Fundamental Photochemical Relationships. The Reciprocity Law. The Photochemistry of Adaptation. (Dark Adaptation. Bright Adaptation.) Receptor Basis of the Fechner Relationship. (Interpretation of the Secondary Process. Basis of the Idioretinal Light. Other Possibilities.) The Representation of Brilliance in the Optic Nerve Process. Multifibral Correlations of Brilliance. Hecht's Theory of the Acuity-Intensity Law. General Implications of Hecht's Theory. Retinal Causes of Contrast. Temporal Phenomena and Visual Diffusivity. The Significance of Charpentier's Bands. *Section 57 — Monocular Stimulus Relations of Chroma:* Statement of the Problem. *I. Chroma and Wave-Length:* Naming the Spectral Chromas. The Spectral Chroma Scale. The Purples. Saturation as a Function of Wave-Length. *II. Chroma as a Function of Wave-Length Composition:* The Psychophysics of Two-Component Mixtures. (With One Extreme Long-Wave Component. Complementaries. With One Extreme Short-Wave Component. Other Cases of Two-Component Mixture.) The System of Spectral Complementaries. The Psychophysics of Three-Component Mixtures. The Color-Mixture Triangle. Abnormal Color-Mixture Relations. Brilliance Relations of the Color-Mixture System. *III. Chroma as a Function of Intensity:* Saturation and Intensity. (The Photochromatic Interval. Intensity Conditions for Maximal Saturation.) Hue and Intensity. (The Bezold-Brücke Effect.) *IV. Chroma as a Function of Spatial Factors:* Areal Functions. Pattern Functions; Chromatic Contrast. *V. Chroma as a Function of Temporal Factors:* Laws of Rise and Decay. Chromatic Adaptation Phenomena. Complementary After-Images. (Recovery.) Chromatic Dimming and Allied Effects. *Section 58 — Monocular Refractive Relations of Chroma:* General Principles. Effects on Hue and Saturation Functions. Color-Mixture Functions. Spatial Effects. Temporal Features. *Section 59 — Monocular Neurological Relations of Chroma:* A General View of the Problem. The Three-Component Theory in Modern Form. Easy Explanations by the Three-Component Theory. Difficulties Encountered by the Three-Component Theory. Contrast and Color-Blindness According to the Three-Component Theory. The Hering Theory in Modern Form. The Ladd-Franklin Theory and Nerve Current Modulation. *Section 60 — Binocular Sensory Relationships:* Corresponding Ocular Regions. Retinal Rivalry and Binocular Color-Mixture. Binocular Flicker Effects.

CHAPTER PAGE

XV. AUDITORY SENSATION 206

Section 61 — Component Auditory Sensation: Definition of the Problem. Nature of the Auditory Stimulus. Acoustic Loudness. Method of Analysis. Loudness as a Function of Frequency. Loudness as a Function of Intensity. Loudness as a Function of Frequency Composition. (Auditory Masking.) Pitch as a Function of Frequency. Pitch as a Function of Intensity. Pitch as a Function of Frequency Composition. Brightness and Its Functional Relationships. Sensory Dependencies of Volume. Stimulus Relationships of Noise. Sensory Correlations of the Vocables. *Section 62 — Composite Auditory Sensation:* Composition as a Function of Frequency and Intensity. Composition as a Function of Stimulus Complexity. (Combinational Tones. Beats and Intermediate Tones. Difference Tones. Summation Tones and the Total Complex.) Auditory Fusion. (Clangs. Consonance and Dissonance.) *Section 63 — Temporal Auditory Sensation:* General Discussion of the Problem. Critical Interruption Frequencies for Tones. After-Effects and Adaptation. Auditory Beats. Music and Speech. *Section 64 — Psychophysiological Relationships of the Auditory Sense-Organ:* The Structure and General Dynamics of the Ear. Theories of the Basilary Response. The Dynamics of the Inner Ear. Basilary Relations of Pitch and Loudness. Basilary Relations of Brightness and Volume. The Resolution of the Laws Governing Loudness. The Resolution of the Laws for Pitch. The Basilary Basis of Fusion. The Basilary Foundations of Vocables and Noises. *Section 65 — Afferent Neurological Relationships of Auditory Experience:* Audio-Frequencies in the Nerve Impulse. Neural Foundations of Auditory Quality. Neural Conditions for Noise. Neural Foundations of Brightness and Volume.

XVI. THE CHEMICAL SENSES 261

Section 66 — Olfactory Sensation: The Action of Odorous Vapors in the Nose. Chemical Determinants. (Position in the Periodic Table. Formation of Organic Compounds. Physicochemical Properties. Odors of Organic Series.) Olfactometry and Absolute Thresholds. Results of Olfactory Mixture. *Olfactory Quality as a Function of Chemical Composition:* Olfactory Quality and Molecular Form. Zwaardemaker's and Henning's Systems. Qualities of Mixtures. Temporal Relationships of Olfactory Intensity and Quality. (Olfactory Rivalry. Olfactory Adaptation.) *The Psychophysiology of the Olfactory Receptor Process:* Review of Possible Means of Receptor Stimulation. The Adsorption Hypothesis of Olfactory Stimulation. The Neural Basis of Olfactory Quality. *Section 67 — Gustatory Sensation:* Gustatory Quality as a Function of Stimulus Characteristics. (Sweetness. Saltiness. Sourness. Bitterness. Quality and Concentration. The Taste of Mixtures.) Gustatory Intensity as a Function of Stimulus Characteristics. Gustatory Quality and Intensity as Functions of Spatial Features of the Stimulus. (Position. Area. Contrast.) Gustatory Quality and Intensity as Functions of Temporal Features of the Stimulus. (Reaction Times. Critical Frequency. Adaptation and Selective Changes.) The Psychophysiology of the Gustatory Receptor Process. (The Taste-Buds. Specific Gustatory Membrane Structures. Sour and Salt. Sweet. Bitter.) Neurological Correlations of Gustatory Quality.

CHAPTER PAGE

XVII. THE CUTANEOUS SENSES 296

Head's Theory of Protopathic and Epicritic Sensibility. Criticisms of Head's Theory. *Section 68 — Thermal Sensation:* The Definition of the Thermal Stimulus. Thermal Experience as a Function of Temperature. (Paradoxical Cold and "Heat.") Thermal Experience as a Function of Spatial Factors. Thermal Experience as a Function of Temporal Aspects of the Stimulus. (Reaction Times. Adaptation.) The Identity of the Thermal End-Bulbs. Hypotheses Regarding the Thermal Receptor Process. (The Case for Warmth. The Case for Cold. Relations of Warmth and Cold Response.) Neurological Correlations of Thermal Experience. *Section 69 — Tactual Sensation:* The Nature of the Tactual Stimulus. Tactual Quality and Intensity as Functions of Stimulus Magnitude. Tactual Intensity as a Function of Stimulus Area. Tactual Quality and Intensity as Functions of Temporal Aspects of the Stimulus. (Tickle. "Vibration Sense." Positive After-Effects. Adaptation.) Composite Tactual Sensation. The Correlations of Experience and the Tactual Receptor Process. (The Receptors. The Operation of the Pressure Gradient. Tickle.) Tactual Experience as a Function of the Afferent Nerve Currents. (Spatial Configurations. Temporal Patterns.) *Section 70 — Cutaneous Pain Sensation:* The Pain Stimulus. Algesic Experience as a Function of Stimulus Magnitudes. Temporal Correlations of Pain. Composite Algesic Sensation. Algesic Experience as a Function of Receptoral and Neural Factors. (Action of Free Nerve-Ends. Spinal Paths for Pain.)

XVIII. KINAESTHETIC AND INTERNAL SENSATION 329

Section 71 — Absolute Kinaesthetic Sensation: The Stimuli to Absolute Proprioceptive Response. The Proprioceptive Sense-Organs of the Inner Ear. (The Semicircular Canals. The Utriculus and Sacculus.) The Mechanisms of the Sense-Organs. Psychophysiological Correlations of Inner Ear Response. Neural Relations of Absolute Kinaesthesis. *Section 72 — Relative Kinaesthetic Sensation:* Kinds of Relative Kinaesthesis. Stimuli to the Musculoskeletal Proprioceptors. Attitudinal Experience as a Function of Stimulus Factors. (Evidence for Articular Sensibility. Thresholds.) Tensive Experience as a Function of Stimulus Factors. (Adaptation.) Exertive Experience as a Function of the Stimulus. Musculoskeletal Proprioceptive Processes and Their Correlations. Neural Correlations of the Relative Kinaesthetic Experiences. *Section 73 — Internal Sensation.*

XIX. GENERALIZATIONS CONCERNING SENSATION 349

Foundations of Intensity and Quality. Spatial and Temporal Determinants.

NOTES 351

Note A — The Introspective Psychology of Color: The Definition of Color. The Classification of Colors. The Achromatic Series. The System of Chromatic Colors. The Psychological Color Solid. The Psychological Primaries. Boundaries of the Color Solid. Other Color Attributes. *Note B — Auditory Qualities and Their Attributes:* The Classification of Auditory Elements. The Attributes of Tones. The Properties of Noises. *Note C — Olfactory Qualities and Their Classification:* Classifications of Odors. Henning's Olfactory Prism. *Note D — Gustatory Qualities and Their Relationships:* The System of Gustatory Qualities. *Note E — The Classification of*

CHAPTER PAGE

Contact Qualities: Psychological Basis of Analysis in This Field. *Note F — The Analysis of Kinaesthetic Experience:* Classification of Kinaesthetic Experiences. *Note G — Internal Experiences and Their Psychophysiological Relations:* The Classification of Internal Perceptions. Desires. (Hunger. Thirst. Lust. Excretory and Secretory Desires. The Desire for Air.) Gratifications and Fatigues. (Gratifications. Fatigues.) Specific Illness Perceptions, and Coenaesthesia. (Nausea. Coenaesthesia.) Patterns of Organic Experience. "Referred Pain."

BIBLIOGRAPHY 371

INDEX 387

LIST OF ILLUSTRATIONS

FIGURE PAGE

28. Schematic Diagram of the Response Arc . . . 9
29. Diagram of a Nerve Fibre in the Unexcited State 20
30. Diagram of a Nerve Fibre in the Excited State . 23
31. Diagram of a Possible Nerve Membrane Mechanism 26
32. Curve of Recovery of Excitability of Nerve After a Previous Stimulus 31
33. To Show How Radiation Is Produced by Stopping the Motion of an Electrical Particle . . 57
34. Curves Showing Black Body Intensity Distributions at Various Temperatures 60
35. Curves Showing Spectral Reflection and Transmission Characteristics of Various Substances 65
36. Brilliance as a Function of Wave-Length . . 67
37. The Scotopic and Photopic Visibility Curves of Human Vision 73
38. Brilliance as a Function of Stimulus Intensity 77
39. The Relative Threshold as a Function of Stimulus Intensity for Vision 78
40. Visual Acuity as a Function of Stimulus Intensity 86
41. Brilliance as a Function of Stimulus Time Conditions 90
42. Critical Flicker Frequency as a Function of Stimulus Intensity 92
43. Cross-Section of the Human Eye 98
44. A Diagrammatic Section of the Human Retina . 102
45. Retinal Rod and Cone Cells 103
46. Diagram to Show the Optical Action of the Eye 106
47. Spectral Absorption Curve for the Ocular Media 109
48. Dependency of Pupillary Size upon Stimulus Intensity 111
49. The Retinal Blood Vessels 114
50. The Course of Dark Adaptation in the Human Eye 124
51. Distribution of Thresholds Required to Explain the Data of Visual Acuity, According to Hecht's Theory 133

FIGURE PAGE
52. THE DEPENDENCY OF SPECTRAL CHROMA UPON WAVE-LENGTH 143
53. WAVE-LENGTH DISCRIMINATION AS A FUNCTION OF WAVE-LENGTH 144
54. WAVE-LENGTH DISCRIMINATION FOR DICHROMATICS . 146
55. THE DEPENDENCY OF SATURATION UPON STIMULUS PURITY 148
56. WAVE-LENGTHS OF COMPLEMENTARY SPECTRAL STIMULI 153
57. THE COLOR-MIXTURE TRIANGLE IN RELATION TO TRIDIMENSIONAL COÖRDINATES 158
58. THREE-COLOR MIXTURE RATIOS TO MATCH SPECTRAL HUES 160
59. COLOR-MIXTURE TRIANGLE WITH SPECTRAL LOCUS OUTSIDE 161
60. RECONSTRUCTED COLOR-MIXTURE TRIANGLE . . 162
61. COLOR-MIXTURE CURVES IN TERMS OF LUMINOSITY VALUES 164
62. RELATIVE LUMINOSITIES OF SPECTRAL COMPLEMENTARIES 166
63. DISTRIBUTION OF THE FOVEAL PHOTOCHROMATIC INTERVAL IN THE SPECTRUM 168
64. DIAGRAM TO SHOW THE BEZOLD-BRÜCKE PHENOMENON 170
65. FLICKER-PHOTOMETER FREQUENCY AS A FUNCTION OF WAVE-LENGTH 179
66. EXAMPLES OF ACOUSTIC DISTRIBUTION CURVES . . 208
67. AUDIBILITY AND TACTILE THRESHOLDS AS FUNCTIONS OF ACOUSTIC FREQUENCY 211
68. LOUDNESS AS A FUNCTION OF ACOUSTIC FREQUENCY 212
69. LOUDNESS AS A FUNCTION OF ACOUSTIC INTENSITY . 215
70. ACOUSTIC INTENSITY THRESHOLD AS A FUNCTION OF INTENSITY 216
71. LAWS OF MONAURAL MASKING 218
72. PITCH AS A FUNCTION OF ACOUSTIC FREQUENCY . 220
73. RELATIVE ACOUSTIC FREQUENCY AS A FUNCTION OF FREQUENCY 221
74. EXAMPLES OF NOISE STIMULI 224
75. ACOUSTIC ENERGY DISTRIBUTION IN CHARACTERISTIC VOWEL SOUNDS 227
76. FORMANTS OF VOWEL AND CONSONANT SOUNDS . . 228
77. SENSORY EFFECTS OF BITONAL STIMULI 233

FIGURE PAGE
78. THE MECHANISM OF THE HUMAN EAR 241
79. DIMENSIONS OF THE BASILAR MEMBRANE AND ASSOCIATED PARTS 242
80. TRANSVERSE SECTIONS OF THE HUMAN COCHLEA AND ORGAN OF CORTI 243
81. DISTRIBUTION OF ACOUSTIC FREQUENCIES ALONG THE BASILAR MEMBRANE 251
82. SECTION OF THE HUMAN NASAL PASSAGES . . . 263
83. CURVES OF OLFACTORY ADAPTATION 273
84. OLFACTORY RECEPTORS 275
85. DISTRIBUTION OF GUSTATORY SENSIBILITY OVER THE TONGUE 286
86. GUSTATORY PERSISTENCE CURVES 289
87. TASTE-BUD AND OTHER RECEPTIVE SYSTEMS . . 291
88. THERMAL RESPONSES OF THE SKIN 303
89. RECEPTORS OF THE SKIN 306
90. KRAUSE END-BULB FROM THE HUMAN CONJUNCTIVA 308
91. FREE NERVE ENDINGS 327
92. STRUCTURE OF THE MEMBRANOUS LABYRINTH . . 330
93. RELATIONSHIPS OF THE SEMICIRCULAR CANALS . . 331
94. AMPULLA AND CRISTA ACUSTICA 332
95. TYPICAL MUSCULOSKELETAL APPARATUS . . . 338
96. A MUSCLE SPINDLE 345
97. GOLGI ORGAN FROM HUMAN TENDON 346
7. COLOR CIRCLE, SHOWING THE RELATIONSHIPS OF COLORS OF A SINGLE BRILLIANCE VALUE 353
8. THE PSYCHOLOGICAL COLOR SOLID 354
9. COÖRDINATES OF THE TONAL MANIFOLD . . . 358
11. THE OLFACTORY PRISM, ACCORDING TO HENNING . 361
12. THE GUSTATORY TETRAHEDRON, ACCORDING TO HENNING 362
13. THE MANIFOLD OF CUTANEOUS SENSIBILITY . . 363

PART FOUR

SENSATION: CONSCIOUSNESS AND THE AFFERENT ARC

Chapter XIII

The Concept of Sensation

Section 50

THE GENERAL NATURE OF SENSATION

217. Current Definitions of Sensation. — In the previous volume of this book, we have considered, under the name of perception, the principal indirect psychophysical relationships which obtain between experience and the so-called objective phase of the response process. We have defined this phase as ending approximately at the surface of the sense-organ, and as beginning at any convenient point in the chain of environmental events which lead to sense-organ stimulation. We must now embark upon the task of studying the analogous relationships which hold between experience and certain succeeding stages of the response propagation. These begin where the objective phase leaves off, and extend to the point of incidence of the propagation upon the sensory projection areas of the cerebral cortex.

We have already noted that a certain degree of flexibility may conveniently be allowed in the location of these two subdivisions of the response chain, since they are to a considerable extent arbitrary in nature. The cardinal feature in the series of events which is concerned in the study of perception is the external physical object. The corresponding feature for the study of sensation may be taken as the *receptor process* or mechanism. But, in order to understand this process, we must discuss it in association with the stimulus — and the sense-organ modifications of the latter — and also in its relation to the afferent nerve currents which it arouses. It is evident that in the case of sensation, as in that of perception, we must deal successively with a series of separable stages in the chain of physiological events, and that the relationships of the experience to these stages will differ with the identity of the latter.

Now, it is evident that this conception of sensation differs rather definitely from that which is current among the majority of contemporary psychologists, although their actual practice in the discussion of the topic conforms, to a marked degree, with the interpretation which we have advocated. The term, sensation, is used by Titchener, and many others, to designate a certain class of so-called elements of consciousness. Extreme sensationalistic psychologies have regarded consciousness as being exclusively a mosaic of sensory atoms, sensation thus being conceived as the fundamental stuff out of which experience is composed. Titchener[331] in his *Outline of Psychology* says: ". . . every idea can be resolved into elements, *i.e.,* elemental *processes;* and these elements are termed *sensations.* . . . We may compare the sensation, the element of the idea, to the elements treated of in chemical science. The idea is a compound; it consists of a number of elemental processes, travelling side by side in consciousness: it therefore resembles the compound bodies analyzed in the chemical laboratory. But the sensation resists analysis, just as do the chemical elements, oxygen and hydrogen. It stands to the idea as oxygen and hydrogen stands to water." But, ultimately, Titchener refers to the "bodily conditions" of these elements, and defines sensation formally as "those elemental conscious processes which are connected with bodily process in definite bodily organs," the latter apparently being sense-organs.

In the *Text-Book,*[332] Titchener distinguishes between three classes of elementary processes: sensations, images and affections. Sensation is now defined as "an elementary mental process which is constituted of at least four attributes, — quality, intensity, clearness and duration." The correlation with bodily organs is no longer included in the definition, but the actual presentation of the facts of sensation in the book still involves stimuli and sense-organs in practically every instance.

James attempted to distinguish between sensation and perception by identifying the former with the processes which appear in consciousness when the afferent nerve currents arouse a minimum amount of " reproductive " activity in the cortex.[333] He is very insistent, however, that "*a pure sensation is an abstraction* . . ." and that " when we adults talk of our ' sensations ' we mean only one of two things: either certain *objects,* namely simple *qualities* or *attributes* like *hard, hot, pain;* or else those of our thoughts in which acquaintance with these objects is least combined with knowledge about the relations of them to other things. As we can only think or talk about the relations of objects with which we have *acquaintance* already, we are forced to postulate a function in our thought whereby we first become aware of the *bare immediate natures* by which our several objects are distinguished. This function is sensation." Here, again, there is a reference to objects and nerve currents, but a tendency to contest the explanation of experience in terms of a synthesis of " mind stuff " atoms.

The view that sensation as a basic mental element is a theoretical abstraction, appears to have been accepted by the majority of modern psychologists.[334] It is commonly admitted that, under certain conditions, we may approximate pure sensation, but that, ordinarily, consciousness is given directly as an integrated system, so that elements must be found by a more or less destructive analysis. Thinkers belonging to the *Gestalt,* and allied modern schools, repudiate the analytical method altogether and, with Ogden,[335] are inclined to answer, " No." to the question: " Are there any sensations? " According to Ogden, so-called sensations are really only attributes, so that we have no justifiable ground for regarding consciousness as being composed of real elements.

218. Sensory Psychophysiology, and Analysis. — Now, we have already discussed this problem of analysis, and have maintained that the method is legitimate, if its results are properly interpreted. However, there seems to be no satisfactory basis for classifying alleged components of experience as sensations, if we adhere to a strictly introspective standpoint. Titchener[336] encountered serious difficulties in distinguishing between sensations and images. Implicitly, his distinction is based upon a psychophysiological criterion; the sensation is correlated with a stimulation of the sense-organs, whereas this condition is absent in the case of the image, although the two mental phenomena may be introspectively identical. This situation, of course, is exactly what we should anticipate on the basis of the monophasic, cerebral determination of consciousness. Given certain cerebral conditions, the consciousness is completely determined, and it makes no difference, introspectively, whether these conditions are due directly to afferent nerve currents or whether they are centrally controlled. Nevertheless, we are forced to deal scientifically with a vast mass of information which correlates experience with stimulus, sense-organ, receptor, and afferent nerve variables. As we have previously noted, these are the facts which every psychologist discusses in his chapters on sensation. Why, then, should we not eliminate the question of analysis from our definition of sensation and restrict the latter to the correlations between experience and the various factors on the afferent arc? Whatever may be the objection to this procedure, it is at any rate the one which we shall follow in the present book.

In view of our previous statements, this decision cannot be interpreted as a sign of agreement with those who deny the possibility of introspective analysis. In fact, we shall find that the study of sensation, along the lines indicated by our definition, inevitably demands such analysis. This is the real reason why sensation has been treated as essentially analytical in nature, but the cart has been put before the horse. The processes of the central nervous system are characterized, in general, by integrative relationships, but those of the afferent arc are highly discrete and functionally isolated from one another. The response propagation may be considered as being unified at the object and also in the cerebrum, but it divides into thousands, and even millions, of distinct paths in the afferent sector of the nervous system. Consequently, when a study of the psychophysiological correlations of the factors in this region is made, we are obliged to atomize and anatomize experience, by picking out those aspects of the latter which correlate particularly with various small subdivisions of the afferent system.

However, it would be surprising if an analysis which is based entirely upon sensory functions in this way, should agree entirely with one which proceeds upon a purely introspective method. As a rule, the aspects which are picked out by the psychophysiological procedure will not be elements, but attributes, as Ogden indicates. This means simply that they will be modes of variation of experience in correlation with certain physiological factors. In certain cases, they may turn out to correspond with real psychical elements, in the sense that they do not inhere in or imply any other factors of experience apart from themselves; but this result cannot be guaranteed.

Moreover, if we define the study of sensation as that of the indirect determinative functions which link the afferent arc processes with experience, we are evidently not restricted to elements or components. Correlations of this sort must, of course, exist for psychical features, such as colors, which are introspectively unanalyzable; but they apply equally to the *structures* of experience, both in coexistence and in time. Thus, the pattern of colors in the visual field is determined by the refractive processes of the eye, the retinal image and the mosaic of retinal stimulation as well as of optic nerve excitation. These relationships are ordinarily discussed under the heading of perception, because they involve spatial patterns or compounds of supposed sensations, but the method of our treatment will compel us to deal with them under the caption of sensation. They are perceptual for us only insofar as they relate to the objective phase of the response propagation. They are sensory in their correlations with the stimulus, sense-organ, receptor and afferent nerve processes.

Exactly similar propositions obviously apply to *temporal variations* in consciousness which are referable to changes in the afferent arc processes. Consequently, we may divide our discussion of sensation under three headings: as (1) component, (2) composite and (3) temporal (or temporally conditioned). It will be most convenient, however, to treat these three aspects under each sensory department, rather than to employ the method which has been used in our discussion of perception; in which the sensory channels were subordinated to the more general categories. The reason for this change of method lies in the existence of a greater continuity between the various aspects of the single sense departments, in the case of the afferent arc, than in that of the objective phase of the response.

219. Various Further Aspects of Sensation. — The definition of sensation, which we have advocated above, harmonizes with the almost unescapable connotation of the sense-organ in any reference to sensation, and it permits us to avoid the difficulty that if we define sensation in purely introspective terms, we are forced to acknowledge the possibility of sensations which have no relation to peripheral processes. Our definition differs from that which is indicated by James, in that we are not forced to strip experience artifically of any of its centrally determined aspects. We accept experience just as we find it, and see what changes occur when various factors in the afferent arc series are subjected to variation. The correlations which are established in this way are sensory, regardless of the nature of accompanying central determinants. It is, of course, to be expected that the latter will enter into the functional equations, but they will be constant in any given case. For some species of relationships, they may turn out to be constant for a large group of cases. The practical reason for adopting this view regarding sensation is that the situation which it envisages is identical with the one in which we make sensory experiments in the psychological laboratory. We have no means, in these experiments, for eliminating the "reproductive" activities of the cortex and, in general, we do not begin with an introspective analysis into elements. We merely pick out certain physiological sensory conditions, vary them, and note the accompanying phenomena in consciousness.

It is much easier, in harmony with the above views, to define *the science of sensation* than to define sensation. Sensation, as a substantive, might be identified with the psychophysiological relationships which are established by the science in question. The sensation of red, in accordance with this view, would consist in the functional relationships holding between red, as a quality in consciousness, and the corresponding characteristics of radiant energy, optical refraction, retinal reaction, etc. According to this conception of sensation, the latter could have no meaning in consciousness considered by itself. Sensation might be given a definite, purely introspective, meaning, by identifying it with the mode of variation of consciousness with respect to the given afferent arc factors. Such a definition of sensation might be formulated by saying that it consists in the derivative, or rate of change, of consciousness with respect to the factor or factors in question; although this concept would have to be interpreted qualitatively as well as quantitatively. The sensation would consist in the kind, as well as the amount of the change in consciousness for a unit change in the given physiological variable. This change would establish a definite direction of modification which could be identified with the sensation as a psychical dimension or attribute. This amounts to a proposition which permits the freest possible use of the term, sensation, as a substantive, namely, that sensation is the aspect of experience which varies as a function of the specified afferent arc factor, in any given experiment. But we shall have little use for interpretations of this sort.

Since the days of the British empiricists, nearly all psychologists have regarded the study of sensation as a very fundamental part of psychology. As a rule, the discussion of this subject has preceded all others, and has furnished the basis upon which other chapters such as perception, memory, etc. could be developed. Extreme sensationalism or empiricism looks upon all of the constituents and aspects of experience as being dependent ultimately upon sensory excitation. In terms of the theory of the central determination of consciousness, this doctrine implies that nothing definite would ever happen in the cortex, if it were not for the influx of specific nerve currents which are generated in the receptors. The actual happenings in the centers are regarded as being determined either by an immediate influx of this character or by residues or impressions left by previous sensory currents. At the present time, the revival of interest in instincts and similar ideas is leading some psychologists to believe in a certain degree of autonomy and even innate impression in the central nervous system. Such writers as McDougall and Hollingworth have practically eliminated the facts of sensation from their text-books. However, the solid facts of psychology are still to be found in this domain, and we shall do well to build our more hypothetical superstructures upon them, now as in the past.

Section 51

THE ANALYSIS OF THE AFFERENT ARC

The afferent mechanism, with which experience is correlated in the sensory manner, can be analyzed in two general dimensions. First, it can be divided into separate sensory departments, according to the nature of the receptor processes and their characteristic stimuli. Secondly, it can be separated into distinct response stages along the line of propagation. Considering the latter form of analysis, we note the following characteristic stages: (1) the stimulus, (2) the sense-organ process, (3) the receptor process, (4) the afferent nerve excitation and (5) the afferent conduction. Each of these stages may itself be capable of subdivision. Thus, in vision, the sense-organ process involves an elaborate series of refractive operations upon the light rays. The afferent conduction phase is ordinarily quite intricate, in the human organism, embracing a number of neurones and synapses, in series as well as in parallel. We may now consider the definition and general nature of each of these five characteristic stages. (See Fig. 28.)

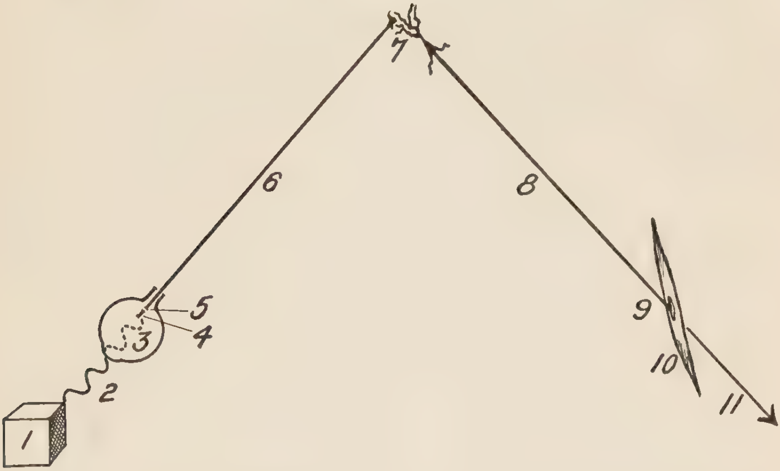

FIG. 28. SCHEMATIC DIAGRAM OF THE RESPONSE ARC.

The figure represents a simplified visual response arc, showing eleven successive stage *positions*, corresponding to the following events: (1) the object, (2) the stimulus, (3) the sense-organ process, (4) the receptor process, (5) the afferent nerve excitation, (6) the afferent nerve conduction, (7) the central adjustor or synaptic process, (8) the efferent nerve conduction, (9) the end-plate process, (10) the effector or muscular reaction, and (11) the effect upon the organism or the environment.

220. The General Nature of the Stimulus. — The stimulus may be defined as the specific physical force, energy or other agency which brings about the stimulation of the given receptive system. It is always possible to characterize the stimulus in general physical terms, which do not explicitly involve any reference to the receptor or sense-organ. However, we cannot identify the stimulus, or its nature, without studying the manner in which the receptor is aroused. A given physical agency is called a stimulus only because it is capable of stimulating. Thus, the stimulus to vision consists of radiant energy of certain wave-lengths, but we can only identify these wave-lengths, and evaluate their capacity to stimulate, by considering their actual relationships to the retina and its correlated processes. In audition, the stimulus consists of mechanical vibrations, at certain frequencies. In touch, it is a pressure gradient upon the skin surface. In taste, it lies in the chemical constitution of dissolved molecules. In some cases, our knowledge of a given receptive system may not be in a sufficiently advanced state to enable us to define the stimulus accurately. This is true, for example, in the case of smell.

The term, stimulus, is sometimes used in a very general sense to stand for the entire set of objective conditions under which a sensory response is set off. Thus, an object or a complicated social situation, may sometimes be called a stimulus. However, our usage of the term will be restricted technically to the actual forces, etc., which set off the receptors. Ordinarily, these are not objects, but are conditions which must be expressed in more or less abstract physical or chemical terms. For example, the stimulus to thermal response is not a hot or a cool object, but a depression or an elevation of the temperature of the skin with respect to a specified standard value. As we have already noted, there are some cases in which the same physical agency extends continuously from the environment into the receptive surface. This is the case with the light rays in vision, and with sound in hearing. Under such conditions, we have preferred to treat that portion of the energy train which is located externally to the sense-organ, as a part of the objective phase of the response, restricting the term, stimulus, to that section of the train which is actually in contact with, or penetrates, the sense-organ. Thus, the visual stimulus consists of light after it has entered the corneal surface; and the auditory stimulus resides in the pressure variations within the external auditory canal, close to the tympanum.

221. The Sense-Organ Process. — The sense-organ process might be held to include the receptor activity as well as other features. However, we shall choose to distinguish between these two stages of the response. The sense-organ process involves a molding or modification of the stimulus, so that it arrives at the receptors in the most useful form. Thus, in the visual instance, the light rays are refracted so as to create a distinct image upon the retinal rods and cones; in audition, the mechanical vibrations are transmitted from the tympanum to the basilar membrane where they can be subjected to resonant analysis. The taste buds and papillæ of the tongue afford enclosures for the occlusion of sapid substances. However, in some departments of sensory response, it is difficult to identify a distinctive sense-organ process. For example, in the field of cutaneous sensibility, the various kinds of end-bulbs which are found would naturally be classed as receptors, and the only auxilliary device appears to be the skin, itself. In olfaction, possibly, we should regard the nose or its cavities as sense-organs but the stimulus acts very directly upon the olfactory receptors, without any essential modification by the nasal apparatus.

222. The Receptor Process. — In practically all cases of response, we can identify a definite species of cell which serves as the receptor, or first point of neural action of the stimulus. The receptors differ anatomically from the afferent conduction fibres, although sometimes they are continuous with the latter. Thus, in vision, we find the retinal rods and cones; in audition, the auditory hair-cells, in smell and taste, the olfactory and gustatory hair-cells, respectively; in cutaneous response, various corpuscles, end-bulbs, etc. The majority of these receptors belong to a histological classification which is intermediate between epithelial and true nervous tissue. Their function is evidently to hypersensitize the ends of the conducting nerves to particular physical forces or conditions, and, possibly, to blunt them to the action of other forces. They are thus, at once, sensitizers and selectors. We cannot doubt that each one of these specific end-organs possesses a very definite and delicate system for carrying out its particular functions. However, there is at least one instance — that of the end-organs for pain — in which no distinct receptor elements are present. In this case, the stimulus acts directly upon the conducting nerve tissue, although it is likely that the nerve-ends are specially differentiated in some way. We shall consider the problem of the general nature of receptors in further detail in the ensuing section, and shall discuss the specific mechanisms of different receptors in conjunction with particular departments of sensation.

223. The Nerve Excitation and Conduction. — The final steps in the afferent arc process consist in the excitation of the essential conducting fibres, and the transmission of an impulse, or a series of impulses, to the brain. Technically, we are compelled to distinguish between the excitation and the conduction. The receptor process must give rise to conditions or forces which are capable of stimulating the conductor; and in this way the receptor cells act as force transformers. Presumably, the characteristic stimuli to the conductors are changes in electrical potential, and when such changes or differences reach appropriate magnitudes, impulses are set off in the fibres, in accordance with principles which are more or less general for all such tissues. We shall consider these principles in detail in the ensuing section. In many instances, as already noted, the afferent conduction path is quite complex and it may be necessary to consider a number of different stages along the path, in order to arrive at a complete understanding of its psychophysiological relations.

Some hesitation may well be felt when we face the problem of designating the exact termination of the afferent arc. The lines of conduction through the cerebrum are known to involve a complex series of neurones, so that the cerebral process, itself, can be divided into afferent and efferent sections. However, in general, we shall include all these stages under the concept of cerebration, and shall regard the afferent arc as terminating at the first point where we can consider the process as becoming cerebral in character. This point will probably be characterized by the introduction of integrative and reproductive factors.

224. The Various Departments of Sensation. — Since the problem of sensation, as we have defined it, is psychophysiological, it is natural that the classification of sensory data should be controlled to a large extent by physiological criteria, rather than upon the basis of pure introspective analysis. Experience can be divided into numerous departments, such as the visual, the auditory, the tactual, etc., by wholly subjective methods, but it would be very difficult to carry this subdivision as far as is possible upon a psychophysiological basis; and, moreover, such a method of subdivision could only by accident lead to a classification in terms of sensation. In some cases, as in the domain of cutaneous sensation, introspection provides us with indispensable criteria for the identification of separable receptor mechanisms. Thus, we have at present no means for distinguishing between the receptors for warmth, cold and touch, except their correlations with consciousness. The separation of the functions of the retinal rods from those of the cones has been possible only on the basis of psychological data. Whether we approach the problems of sensation from the standpoint of the psychologist or of the physiologist, we seem compelled to base our reasoning upon a combination of physical and introspective facts.

Physiologists now recognize the existence of more than twenty different types of receptors in the human nervous system. These individual sensory mechanisms may be grouped into species on the basis of their anatomical nature, the character of their stimuli or, finally, their general biological significance. The second and third methods of classification appear to be the most useful. Biologically, we may follow Sherrington[337] in his classification of receptors into (1) exteroceptors, which are concerned in the adaptation of the organism to objects in its external environment, (2) proprioceptors, which are concerned with the internal regulation of motor activities, and (3) interoceptors, which are involved in the adjustment of the organism to special conditions in internal organs not essentially motor in function. The first two classes of receptors are usually grouped together as somatic receptors on account of the unitary nature of the effector processes which they subserve, these processes being distinct from those which are attached to the visceral or interoceptors. The exteroceptors may be divided into distance receptors and contact receptors, according as the primary objects of the response are at a distance from or in contact with the organism, respectively.

The distance receptive senses of man are vision, audition and smell, the corresponding receptors being respectively the retinal rods and cones, the hair-cells of the inner ear, and the hair-cells of the olfactory epithelium. Other exteroceptive senses, in addition to the distance receptors, are those for touch and pressure, tissue injury (pain), cold, heat, and taste. The identity of the receptors for certain of these senses is a matter of some dispute and will be considered later. The proprioceptive senses include (1) the receptors of the vestibular portion of the inner ear, which are sensitive to orientation and acceleration, and the mechanisms of (2) articular, (3) tendinous and (4) muscular sensibility. The visceral or interoceptive systems include those for the feelings of hunger, thirst, nausea, and the desires to micturate and to defecate. Responses to abnormal states of the respiratory, circulatory, digestive, and other internal organs are also embraced in this class. The specific sensibilities of the sex-organs, and possibly those of taste, appear to lie on the boundary between the contact and interoceptive classes.

In presenting the psychophysiological facts relating to these various departments of sense, we shall follow the order which has already been employed in our exposition of the facts of perception, beginning with senses which have the most external reference and ending with those whose concern is most internal. This order, which has been employed by Titchener [338] and others, favors a demonstration of the differences and also of the similarities between the various sensory systems. It enables us to arrange the sense departments into a functionally continuous series.

Section 52

THE PHYSICAL NATURE OF NERVE PROCESSES

225. The Present Status of Nerve Physiology. — That portion of the study of sensation which is concerned with the relationship between experience and the stimulus can be carried out in the absence of any knowledge of the nature of nerve action. But we cannot *complete* our study without definitely concerning ourselves with the details of this latter process. The first stages in the receptor response are not essentially nervous, but if the function of the receptor is to convert special energies into a form which can act upon conducting nerves, one can hardly hope to understand even the receptor process without some knowledge of the mechanism of neural excitation. When we come to consider the conductors themselves, the physiological factors with which we must deal become exclusively neural in character. They remain in this category throughout the discussion of cerebration, and also for the first steps in the efferent arc, in the treatment of action. Consequently, it is necessary for us to review modern knowledge concerning this all-important topic.

It is highly gratifying to note that, at the present time, our knowledge of the nerve process has reached very definite form, and seems to be becoming rapidly more and more detailed. The anatomy of the nervous system had far outstripped its physiology; detailed maps of the courses of neural conductors have been available for many years, and the topography, even of the cerebral cortex, is now established with great minuteness. However, psychologists have hitherto been compelled to discuss the psychophysiological relationships of these structures in the vaguest and most uncertain language. There has been an almost complete absence of reliable guiding principles, and each psychologist has been forced to invent his own concepts. The nervous conductional system has been conceived, since the time of

Descartes, by analogy with a system of pipes or strings; and, even in the twentieth century, we find McDougall and others talking about neurochyme and the like, as if the process could properly be conceived in terms of a fluid flow, involving a substance which can accumulate, drain, overflow, etc.

At the present time, however, it seems that we are entering upon a period in which the psychophysiologist can reason about these matters on a much more reliable basis. The researches of Nernst,[339] Lucas,[340] Adrian,[341] Forbes,[342] and Lillie[343] have provided us with a very definite conception of the nerve process. In some respects, we can visualize it in a more satisfactory manner than almost any other physiological activity. It has been shown to be subject to very definite quantitative laws, some of which can be deduced theoretically from structural hypotheses, after the manner of physical theories concerning inorganic phenomena. The all-or-none law establishes very definite limitations for our arguments in this domain, and proves itself a paramount guiding principle. The Nernst-Lillie picture of the neural responses reduces the latter to ultimate physical terms, and furnishes a satisfactory explanation for all of the main phenomena. Consequently we are justified in proceeding with new courage in an attempt to work out the more intimate relationships between experience and neurological activities. This undertaking begins at the sense-organs, but its goal lies in the region of determination of consciousness, in the cerebral cortex.

226. Methods of Thought Concerning Nerve Psychophysiology. — In pursuing this endeavor, we shall naturally be compelled to employ the method of hypothesis. Unfortunately, we cannot determine the detailed nature of the sensory and central nerve processes, by any available method of direct observation. However, we are in no worse situation in this regard, than is the physicist in relation to the majority of problems which he is endeavoring to solve at the present day. The structures of crystals, molecules, and atoms are even more inaccessible than are those of the nervous system. We can ascertain their intimate character only by a form of experimental reasoning, in which we develop plausible conceptions and see whether their logical consequences check with the facts. These facts, in the psychophysiological situation, are both physical and introspective; in order to develop adequate notions concerning sensory and central nerve mechanisms, we must employ both kinds of data. We must avoid undue affection for theories which may fail to harmonize with all of the facts in question. It is not to be expected that any individual thinker will have a sufficient amount of prescience to advocate hypotheses that will be correct in all of their details, and hence all such views should be regarded as mere steps in a process of research. However, this truth should not frighten us from the advocacy of whatever ideas appear to be the most adequate at any given time. The intellectually more peaceful attitude of agnosticism can result in nothing but stagnation of progress in this domain.

In attempting to work out a satisfactory view regarding nerve activity, we must utilize not only the findings of physiology, but also the concepts and principles of modern theoretical physics. All psychophysiology is ultimately psychophysics, and the importance of ultimate physical concepts probably becomes greater in proportion as the directness of the psychophysiological relationships increases. The lines of thinking which have already been inaugurated by W. Köhler,[344] regarding the electrical aspects of cortical activity, are to be commended highly upon this ground. The colloidal, the chemical and the ionic constitution of nerve substance must inevitably be concerned in ultimate psychophysical correlations. They are also definitely involved in any satisfactory understanding even of sensory response. But nerve physiology also presents us with very pertinent concepts and principles which can be employed to great advantage without necessarily reducing them to their ultimate physical meanings.

From the standpoint of general nerve physiology we find ourselves, to-day, upon the threshold of an epoch of *quantum theorizing* regarding the processes of the nervous system. The all-or-none principle, together with the co-operation of a plurality of insulated conducting units in all such processes, demands that certain aspects, at any rate, of these activities should be interpreted in terms of groups of unit disturbances: individual neural pulses. This conception enables us to deal numerically with these aspects, in a manner which resembles that characterizing the thinking of the physicist and the chemist, with their conceptions of energy quanta, molecules, atoms and electrons. The notion of intensity must be replaced by that of frequency, pulse density, or the like. Qualitative variations in the current units which pass along a given nerve are ruled out. From one standpoint, the principle of specific nerve energies becomes more rigorous than ever before, but from another standpoint we can see possibilities which were excluded by that principle.

227. **The Resting State of the Nerve Cell.** — Nerve cells and fibres consist of minute masses of protoplasmic fluid, surrounded by a thin membrane and containing a nucleus, after the fashion of practically all biological cells. Their capacities for excitation and conduction are derived from similar abilities which are characteristic of living cells in general, but which are developed to an exceptional degree in neural tissues. When acted upon by an appropriate stimulus, the nerve cell transmits an invisible influence along its length, which may give rise to contraction of the muscle units to which it is connected or may yield definite modifications of consciousness. It was for a long time suspected that this so-called "nerve impulse" is essentially electrical in nature, since it is accompanied by a so-called electrical *action current*. However, the latter consists not in the production of electrification in the nerve but rather in the partial disappearance of such a state, which was already present in the resting cell. This manifests itself through the "current of rest," or demarcation current, which is obtained when the cut end or injured surface of a nerve is connected through a galvanometer to the nerve sheath. The current flows from the sheath to the injured portion, indicating that the former

is positively charged with respect to the latter. When the nerve cell is excited, this positive electrification of the sheath momentarily decreases.[345]

The electrical theory of matter, and in particular the so-called theory of "electrolytic dissociation," offers us the materials for a simple explanation of the resting electrification of the nerve. A nerve fibre, like almost any other living cell, consists of an aqueous solution of many substances, both organic and inorganic. Among these are substances which become *ionized* in solution, that is, their individual molecules are broken up into electrically charged particles, positive and negative ones being produced in equal numbers. These particles, in common with all of the molecules of the cell, are endowed with a rapid vibratory motion which represents the temperature, or thermal energy, of the substance. In accordance with the general theory of solutions, the motion of the dissolved particles among the molecules of the solvent, water, resembles that of the molecules of a gas in free space. This means that they must exert a pressure upon any surface which tends to interfere with their free diffusion. Prominent among the ions of this sort are to be counted those of carbonic acid, the substance which is produced by the respiratory function of the cell.

The liquid mass of the cell is contained within a membrane which may be conceived as a more or less solid envelope. This membrane is not necessarily to be identified with the myelin sheath,[346] in the case of the nerve fibre, and it may simply consist in some peculiar condition of the molecules at the surface of the general cell mass. As a rule the bounding surface of a liquid mass behaves like an actual membrane. Now, it is obvious that ions in the general cell mass will exert an outward pressure on this membrane, especially if there is an aqueous medium outside as well as inside of the cell. If the membrane is absolutely tight or *impermeable* to these ions there will simply be a tendency to distend it, but if, on the other hand, the membrane is somewhat porous, certain of the ions may pass through. It is clear that small ions will pass through more readily than large ones, and in the case of those of carbonic acid the hydrogen ions will almost certainly be the smaller. Hydrogen is the smallest of the atoms and its positive ion — the so-called proton — is probably the smallest of all known physical particles. If bare hydrogen ions exist in solution, it is almost certain that no membrane can possibly be formed which will be capable of holding them back since the membrane must itself have a molecular structure. The carbonate ions must be very much larger than are the ions of hydrogen, not only because they contain a number of atoms in combination instead of one, but because the atoms themselves are many times larger than that of hydrogen. It is, therefore, almost *a priori* certain that if a membrane is relatively impermeable the hydrogen ions will still pass through it, while the carbonate ions will be held back.

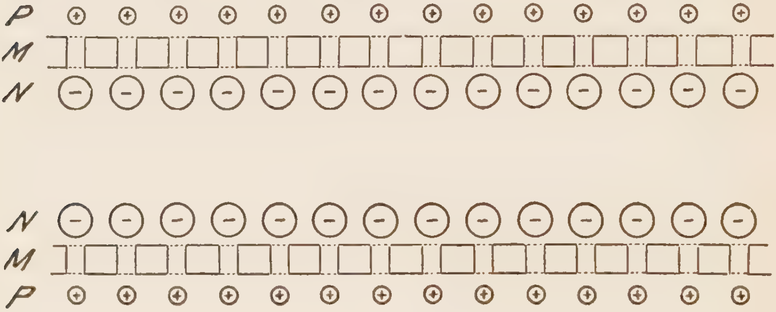

FIG. 29. DIAGRAM OF A NERVE FIBRE IN THE UNEXCITED STATE.

This is a symbolic section of a nerve fibre, showing the polarization layer. *M* represents the porous membrane, *N* the layer of large negative ions, and *P* the outer layer of smaller positive ions, which can pass through the holes in the membrane.

Since the hydrogen ions are by nature positively charged, the outcome of this selective diffusion through the cell membrane must evidently be to form a layer of positive electrical particles on the outside of the cell. On the inside of the cell, there will be a corresponding layer of negative particles, which are held in position by the attraction exerted upon them by the external positive layer. This attraction is mutual and not only causes the diffused positive ions to remain in the immediate vicinity of the membrane but limits the number of them which can pass through the membrane, since, when their concentration on the outside reaches a certain limit, there will be just as many returning into the cell per unit time as leave it. Thus a definite state of equilibrium is established which involves an "electrical double layer," with a magnitude depending upon the exact permeability of the membrane and the internal concentration of the ionized substance. (See Fig. 29.) The existence of this electrical double layer at the membrane may be said to constitute a *polarization* of the latter, such polarization being capable of variations in degree under different conditions.

It is clear that the polarization of the cell membrane, just considered, explains the demarcation current, even the direction of this current corresponding to that theoretically deduced. When an electrical connection is made between an injured and an uninjured portion of a nerve, this connection is virtually established across the cell membrane, so that the mechanism of the latter acts in the same way as an electric "battery." The energy of this "battery" is derived from the compression of the ionized substance inside of the cell, and the continued flow of the demarcation current must involve a diffusion of some substance, *viz.*, hydrogen, through the cell wall. This process is similar to that which occurs in the special form of electrical "battery" known to physical chemists as a "concentration cell."

228. **The Mechanism of Excitation.** — The next problem which we face is that of determining the mechanism of stimulation of the resting cell. It is a familiar fact that an externally produced electric current or voltage provides a very ready means of stimulating nervous tissue. The great sensitivity of such tissue to electric currents is by itself almost conclusive evidence of the essentially electrical nature of the nerve process. The stimulating power of electrical currents, however, depends very radically upon the exact time relations of the current. An alternating current of the

right frequency stimulates more readily than does a direct current, but if the frequency is very high there may be no stimulation at all, even with very large currents. It is found experimentally that the intensity threshold for a given nerve is proportional to the square of the frequency. Nernst [347] succeeded in explaining this relationship mathematically on the basis of an assumption as to the physical conditions underlying the threshold. He supposed that in order just to stimulate a nerve cell, the current acting upon it must polarize the cell membrane to a certain critical degree, this polarization being a natural result of a current flow which piles one kind of ions up on one side of the membrane and draws them away from the other side. By combining this assumption with the known laws of electrical action and diffusion, Nernst arrived at a law connecting the time required to stimulate with the intensity of the stimulus. Although Hill,[348] Lapicque,[349] and others have found it necessary to complicate Nernst's original theory by further details, the quantitative success of his original hypothesis stands out as a unique achievement in the application of mathematical physics to biological phenomena.

It is evident, however, that Nernst's assumption that the physical basis of the nerve threshold is the establishment of a certain degree of polarization in the cell membrane must be modified to fit the fact that the membrane is already polarized before stimulation. It was pointed out by R. S. Lillie [350] that this modification might take the form of a mere change of algebraic sign; in other words, stimulation of the nerve may require a critical *de*polarization of the membrane, this depolarization, although definite in amount, not necessarily being complete. Lillie showed further that this assumption is in harmony with many facts relating to conditions of stimulation of the nervous tissue. It harmonizes first with Pflüger's laws [351] of electrical stimulation, according to which there is stimulation at the negative pole (cathode) upon closing the circuit and at the positive pole (anode) upon opening the circuit. Both of these poles are applied to the outside of the nerve. The cathode may be regarded as spraying the nerve with electrons, which are negatively charged and which consequently combine with the positive particles on the outside of the nerve, neutralizing them and thus depolarizing the membrane. The anode, on the other hand, sucks electrons away from the outside of the cell, thus increasing its production of positive particles. Facts to be considered below lead us to suppose that, under these conditions, the membrane will react in such a way as to compensate for the increased polarization, so that, when the circuit is opened and the auxiliary polarizing force of the anode is removed, a depolarizing action will occur.

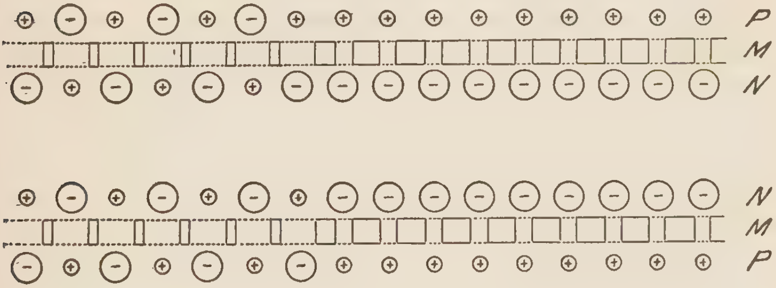

FIG. 30. DIAGRAM OF A NERVE FIBRE IN THE EXCITED STATE.

The general scheme of this diagram is the same as explained under Fig. 29. However, at the left-hand side, the fibre is represented as being in the excited condition, the holes in the membrane being enlarged so that the negative particles can pass through, thus neutralizing the polarization layer in this region.

It is a well recognized fact that anode stimulation at the "break" occurs less readily than cathode stimulation at the "make." (See Fig. 30.)

Stimulation of nerve by many agents, other than the electric current, can also be explained on the assumption that the essential condition of stimulation consists in a certain depolarization of the membrane. One way in which to depolarize the membrane would be to place the cell in a solution, containing positive and negative ions which are similar in physical character to those within the cell itself. Under these conditions, there would be just as much of a tendency for positive ions to pass into the cell as to pass out, so that the production or maintenance of polarization, by the mechanism of selective diffusion above described, would be impossible. This explains the stimulating power of various "electrolytes." It also explains why these substances, including carbonic acid, eventually bring about a permanent depression of activity or "narcosis" in the nerve.

Another method, which is obvious *a priori*, for stimulating the nerve is to injure or destroy the membrane. This depolarizes the latter because negative as well as positive ions are permitted to diffuse through it. So-called "mechanical" stimulation of the nerve is evidently of this sort, depending upon a gross maceration of the cell envelope. The action of certain organic narcotics, chloroform, ether, alcohol, etc., which first excite and then depress the nerve, probably depends upon a chemical destruction or impairment of the membrane. The stimulating effect of other conditions, such as desiccation and heat, can be explained in similar terms.

229. The Mechanisms of the Threshold and of Propagation. — It is evident that the Nernst theory of stimulation, in the modified form outlined by Lillie, demands a "negative variation" of the "current of rest," since depolarization would necessarily manifest itself in this way. It does not follow, however, from any statements made heretofore, that this negative variation will be *propagated* along the cell or fibre from the point of stimulation. Lillie has pointed out that in order to explain propagation of the variation, we must suppose not only that the polarization of the membrane depends upon its differential permeability but that its relative impermeability depends upon its degree of polarization. Polarization and permeability, in other words, are the two essential factors in the nerve process, and they are related to each other in the propagation of the nerve impulse in a manner analogous to the relation of pressure and displacement in the propagation of sound, or the relation of the electric and magnetic vectors in the propagation of light. These relations are all such that a change in one of the quantities always involves a change in the other, the locus of the secondary change not coinciding with or falling wholly inside that of the primary change. This relation necessitates propagation.

It is easy to see why the degree of polarization of the nerve cell membrane should depend upon its degree of permeability, since it was from assumptions regarding the nature of this permeability that we were enabled to deduce the existence of polarization. It is not so obvious, however, why the *permeability* of the membrane should alter when some external force, such as an electric current, brings about its depolarization. A moment's consideration, however, will show that such artificially produced depolarization must have some effect upon the constitution of the membrane. When the polarization is present, the substance of the membrane is subjected to electrical stresses which are represented by parallel lines of force, connecting the positive charges on the outside of the membrane with the negative charges on the inside. In accordance with the general electrical theory of matter, these electrical stresses will necessarily produce some distortion of the molecular or atomic structure of the membrane, which distortion will have a direction determined by the impressed electrical forces. When these forces are removed by depolarization the distortion will tend to disappear. The distortion may well be of such a character as to render the membrane less permeable than would be the case if it were absent. In this event, the depolarization would have the effect of increasing the permeability.

One conception of the molecular structure of the membrane, which has occurred to me,[352] pictures the membrane molecules as being considerably longer than they are wide, with opposite electrical charges on either side in the middle of the molecular length. The individual molecules are conceived to be rotatable, like compass needles, about their centers of mass. The electrical field produced by the polarization will then tend to dispose all of these molecules with their long axes at right angles to the field, *i.e.*, parallel to the plane of the membrane, and in this position they will offer maximal obstruction to any particles tending to move

56525

perpendicularly to this direction. When the polarization field is removed, however, the molecules will tend to swing into a position at right angles to the one just considered, on account of the mutual attractions and repulsions of their charges. In this position they will offer much less resistance to the passage of particles perpendicularly to the plane of the membrane. This mechanism is of course only symbolic, but it illustrates the general principles which must be involved. (See Fig. 31.)

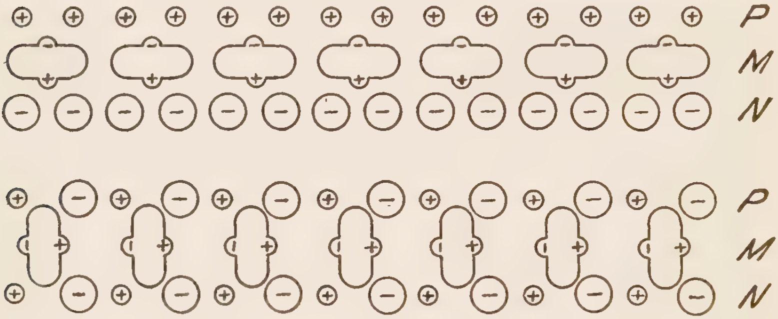

Fig. 31. Diagram of a Possible Nerve Membrane Mechanism.

The oblong units in the diagram, bearing positive and negative charges on their sides, represent the molecules which constitute the substance of the nerve fibre membrane. The small positive and the larger negative circular units represent the ions forming the polarization layer (*cf.* Figs. 29 and 30). In the upper portion of the figure, the membrane is shown in the polarized condition, with the oblong molecules turned by the electrical field of the polarization layer, so as to obstruct the free passage of the larger ions. In the lower portion of the figure, both the polarization and the obstructing power of the membrane are represented as being broken down by a turning of the oblong units.

230. **Special Evidences of Increased Permeability during Excitation.** — Apart from purely physical reasoning, we have an excellent biological basis for assuming that stimulation of a living cell will result in an increased permeability of its enveloping membrane. It is through modifications in the permeability of the latter that the cell regulates the income and outgo of chemical materials. Food substances absorbed from the environment, and waste products excreted, must pass through the membrane and it is to

be expected that both of these transfers of substance will be increased during a state of excitation of the cell, since this latter state involves an augmented chemical activity. Lillie has cited a number of cases in non-nervous cells in which an increased permeability of the cell membrane, resulting from stimulation, can be clearly demonstrated. Modern studies show that the excited nerve cell gives off carbon dioxide and ammonia, and that it also absorbs oxygen and sugar.[353] These interchanges of substance occur to some extent in the unexcited state, but are markedly increased in a region of excitation.

Besides corroborating the idea that the ions of carbonic acid are the ones which are essentially involved in the polarization of the membrane, these facts indicate that the normal permeability of the latter is such as to permit a slight diffusion of carbonate ions, and that the depolarization, accompanying excitation, is the result of an increased permeability to these ions, rather than of a decreased permeability to the positive hydrogen ions. Our theory regarding the cause of the polarization of the cell membrane demands that an increase in the permeability should be followed by a decrease in the polarization, provided the permeability is already practically perfect for the positive ions. That this requirement is fulfilled is indicated, not only by the slight diffusion of carbon dioxide during the resting state, but also by the free permeability of the membrane at all times to water, and the ions of water. The facts which we have just been considering show that this reciprocal relationship between permeability and polarization is a mutual or "symmetrical" one. In other words, they indicate that a decrease in polarization below a certain critical point results in an increase in permeability. The analogy between the principles of the propagation of nervous energy and those for acoustic and radiant energy is thus very close, a change in either one of the two principal variables causing a reverse change in the other variable.

231. **Resistance of the Nerve Cell to Excitation.** — The reciprocal relationship between these two factors in the

case of the nerve impulse is not, however, absolutely symmetrical. It is almost certain that any initial change in the permeability, no matter how small, will result in a reverse change of the polarization, but the fact of the threshold indicates that an alteration of the polarization does not bring about an increase in the permeability until a certain critical depolarization has been developed. Indeed, certain phenomena, which we shall soon consider, indicate that before this critical point is reached there is a tendency for the permeability of the membrane to decrease below normal, as a result of depolarization. The polarization and the permeability of the membrane appear to enter into a system in which there is a point of unstable equilibrium.

The nature of this system can be illustrated by a mechanical analogy which is effective as a classroom demonstration. Suppose that we tip a chair gradually forward by applying a finger to the back of the chair. At first the weight of the chair resists the tipping force, but when the center of gravity passes over the very small base of support the chair parts company with the finger and falls to the floor with a crash. The tipping of the chair up to the point of unstable equilibrium represents the changes in the character of the membrane system which must be produced in order to pass the threshold, while the crashing of the chair to the floor, once the equilibrium point has been passed, represents the liberation of the internal energies of the nerve cell which constitutes the state of excitation. The degree of energy thus liberated is evidently dependent almost wholly upon the inherent nature of the system and not upon the intensity of the stimulus or tipping force.

The laws of the nerve membrane system, formulated in more exact terms, would probably read somewhat as follows: An increase in permeability always produces a decrease in polarization. An initial decrease of polarization, however, first results in a decrease in permeability which tends to compensate for the initial change. But if the depolarization reaches a critical or threshold amount, the "sign" of the change is reversed, so that an increase in permeability results. As soon as this increase begins, the initial depolarization is further augmented by the law which makes polarization depend reciprocally upon permeability, so that the equilibrium of the nerve membrane system is completely upset, the polarization now decreasing to a minimum while the permeability increases to a maximum.

232. **The Basis of du Bois-Reymond's Law and of Electrotonic Effects.** — The supposition that the first reaction of the membrane to a decrease in polarization is a decrease in the permeability, rather than an increase, is in harmony with a variety of facts concerning the nerve function. It explains, among other things, du Bois-Reymond's law [354] of electrical nerve stimulation, according to which a nerve is stimulated only by a change in an electrical current and not by a steady flow of electricity. The investigations of Waller,[355] Hill,[356] Lapicque [357] and others have shown that there is a certain rate of application of an electrical voltage which stimulates the nerve with the least total expenditure of energy. (See discussion of "chronaxy," pages 38–39.) The failure of a slowly applied electric voltage to stimulate — at the cathode — can be understood if the first action of the membrane is in the direction of adaptation or compensation, the mechanism of which involves a decrease of the permeability below normal; thus tending to increase the polarization above normal or to maintain it in the face of an external depolarizing agency. Such an action is evidently a physical possibility if, as we have found reason above to suppose, the normal permeability does not completely interfere with the diffusion of the negative ions, but simply impedes the movement to a certain degree. If the external depolarizing agency is applied very rapidly, the membrane does not have time to develop its compensating reaction, so that the threshold depolarization is reached, and excitation results.

We have seen that the "break" stimulation at the anode is best explained on the assumption that the membrane tends to compensate for the excess of positive ions at the anode, by decreasing its permeability at this point. This is apparently another instance of the general tendency of the membrane to adapt itself to a stimulus, by permeability changes, so as to maintain the resultant polarization constant. Stimulation at the anode upon interruption of the current will follow only if this interruption is sufficiently rapid, since if it is slow the membrane will have time to compensate and the resultant change in the polarization will be insufficient to cause stimulation.

These views regarding the changes in the condition of the membrane at the cathode and anode respectively should lead us to look for some further specific effects of such modifications. The phenomena of "electrotonus" are of this sort. It is to be anticipated that the stimulability, or the stimulation threshold, of the nerve will depend upon the condition of the membrane, in particular upon the dynamics of the equilibrium between its permeability and its polarization, so that a compensating change in the permeability will cause an alteration of the threshold. It is a familiar fact that the stimulation threshold decreases at a cathode while it increases at an anode, indicating in terms of our theory that decreased permeability results in increased stimulability and *vice versa*.

233. Refractory Phase and Allied Conditions. — The above deductions are further borne out by a study of the alterations in stimulability which take place during and after any given process of excitation in the nerve fibre. It is well-known that, after such a fibre has once been stimulated, it cannot again be set into excitation until a certain interval has elapsed, this interval being called that of *refractory phase*. Refractory phase is evidently represented in our physical hypotheses by the state of collapse of the membrane which follows the attainment of the threshold depolarization. If excitation consists in an increase of permeability to a maximum, then it is clear that further excitation is impossible until the original impermeability has been at least partially restored. So long as no restoration whatever has occurred the cell remains in what is known as absolute refractory phase.

The fact that this condition is only temporary proves that a mechanism exists for the restoration of the membrane to normal condition, this mechanism probably being identical with that which enables the membrane to react in a compensating manner to small depolarizing forces. The recovery is gradual and while it is in progress the cell is in a so-called state of relative refractory phase. In this condition, its excitability is depressed below normal, to a degree which is greater the less the recovery which has been achieved at any instant. Since the recovery must consist essentially in a progressive decrease in the

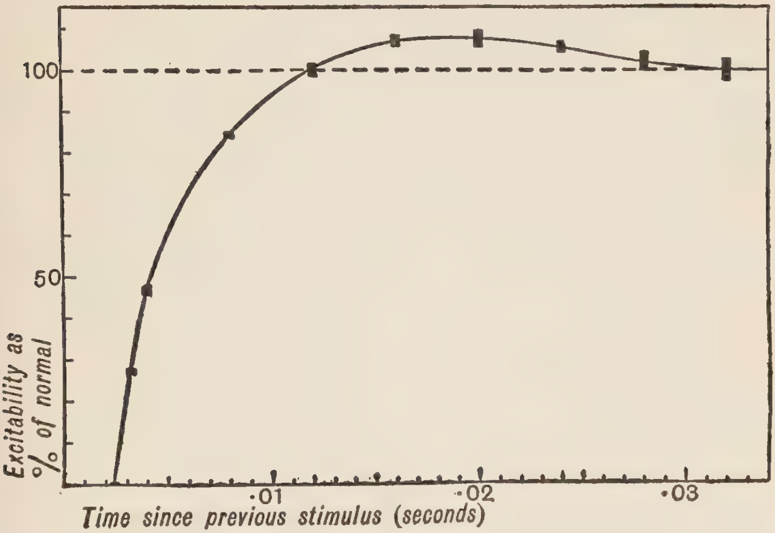

FIG. 32. CURVE OF RECOVERY OF EXCITABILITY OF NERVE AFTER A PREVIOUS STIMULUS.

(This figure is reproduced from Bayliss, Principles of General Physiology, 1915, p. 389.)

The curve shows that immediately after stimulation the excitability is reduced to zero, after which it recovers gradually, reaching the normal condition in about one-eightieth of a second. Under certain experimental conditions, this is followed by a period of temporary excess excitability, as shown, but the latter phase is now believed to be absent in the normal state of the nerve, within the organism.

permeability of the membrane, these facts evidently correspond with the view that excitability is inversely proportional to the permeability in question, or that the threshold of stimulation is directly proportional to it. (See Fig. 32.)

When the liquid medium, in which the nerve fibre is immersed, is in a somewhat acid condition (in excess of "pH 7"), recovery from relative refractory phase is followed by a phase of hyperexcitability during which the threshold of stimulation is *lower* than in the resting state. This overshooting, however, is only relative to a depressed resting value, due to the increased acidity, and never carries the excitability above the maximum for the normal nerve environment. Adrian[358] and others have attempted to account for certain facilitative effects of one stimulus upon another, on the basis of a supposed timing such that one stimulus falls in the period of hyperexcitability left behind by its predecessor. However, recent investigations indicate that this overshooting probably does not occur in the natural state of the nerve cells, within the body, since the acidity is inadequate under these conditions.

The above considerations are evidently in harmony with the facts which indicate that a nerve impulse, set up during a state of refractory phase, has a smaller amplitude or intensity than a normal impulse. The "amplitude" of a nerve impulse must stand either for the amount of change in permeability which results from stimulation, or for the amount of depolarization which is a consequence of this change. It should be clear why these amplitudes vary with the exact level of permeability which exists at the instant of stimulation. If a nerve impulse is represented as a wave of permeability change, referred to normal permeability as a base line, it is evident that a decreased amplitude must stand for an elevation of the troughs of the waves above the base line, whereas an increased amplitude would be referred to a depression of the troughs below the line. The all-or-none principle, which we shall consider more specifically below, can be interpreted to mean that the crests of all waves lie on a constant locus, representing the invariable maximum permeability of the membrane.

234. **The Energetics of Nerve Action.** — It is apparently a necessary consequence of the theory of the physical nature of nervous activity, which has been outlined above, that the process in question should involve metabolism. It seems inevitable that the restoration of the cell membrane to its rest condition, after excitation, should require the expenditure of new energy. This energy must naturally be obtained by the oxidation of some substance present in the cell. It has long been known that oxygen is needed in order to maintain the nerve constantly in a state of excitability. A nerve which is caused to function repeatedly in the absence of oxygen eventually falls into a state of permanent refractory phase, which is exactly what would be expected if oxygen is necessary in order to rebuild the membrane.

It is only recently,[359] however, that experimental demonstrations have been made of the actual utilization of oxygen and fuel substance (sugar) by the nerve, as well as of the generation of heat[360] while in action. The fact that, at the same time, the nerve gives off carbon dioxide and ammonia, indicates clearly that the carbohydrate fuel, along with some protein material, is being oxidized to furnish the energy for the excitation process. Recent studies in this field suggest that nerve metabolism is similar in general nature to that occurring in muscle, although involving very much smaller quantities of energy and materials. It seems likely that the immediate process of recovery of excitation is anerobic, or can go on in the absence of free oxygen, but that the latter is required to maintain the supply of oxidative substances which are concerned in this process.

The amount of heat which is liberated in consequence of nerve action is extremely small. In the case of the frog's sciatic nerve, the rise in temperature is found to be about 2.7×10^{-8} degrees Centigrade for each individual impulse. However, the production of heat is not limited to the moment of passage of the impulse, but continues over a period of approximately ten minutes, yielding a total of about ten times the number of calories which is involved in the passage of the impulse, itself. The total energy per impulse, per centimeter, for a single nerve fibre, is considered to be about 10^{-5} ergs, which greatly exceeds that which is manifest in the electrical action current. It will be recalled that one erg is the amount of energy carried by a mass of one gram moving at one centimeter per second, this in itself being a very small quantity. In the case of the frog's sciatic nerve, stimulated 280 times per second, the total heat production corresponds to the utilization of 0.0008 cubic centimeters of O_2 (oxygen gas) per gram per minute, with a volumetrically equal evolution of CO_2.[361]

The relative indefatigability of nervous tissue is probably a consequence of the very small amount of energy which is required, since the substance of the nerve cell can supply this energy from its stores over a comparatively long period. Thus, a nerve will function in an atmosphere of nitrogen for as long as an hour. It is clear that the oxidation which occurs incidentally to the rebuilding of the cell membrane will compensate for the loss of carbon dioxide from the cell during the process of excitation, so that fatigue will set in only when the fundamental oxidizable material of the cell is exhausted, or the oxygen supply is cut off. In *vivo* these substances will naturally be replenished, while in *vitro* the nerve becomes unfit for experimental tests due to other causes, such as desiccation, long before its metabolic fuel is used up.

The above considerations evidently refute the view, which has sometimes been advocated, that the nerve impulse is a true cyclic process in the thermodynamic sense. Such a process, resembling the propagation of light in free space or of sound in a perfectly elastic medium, involves no loss or gain of energy at any point, the original energy of the stimulus simply being transmitted from one part of space to another. In the case of the nerve impulse, however, each phase of the propagation necessitates the expenditure of a certain amount of energy, which is developed within the phase in question and cannot be transmitted to succeeding phases. The original process of excitation does not involve any significant absorption of the energy of the stimulus, but consists in a trigger action of the latter which releases energies latent within the nerve itself. The propagation of the impulse evidently depends upon the fact that one portion of a nerve can be stimulated by the excitatory state of an adjoining portion, so that the trigger process is repeated at successive points along the nerve path.

235. The All-Or-None Principle. — Modern studies, even when considered apart from theory, make it quite clear that the action of individual nerve fibres follows a principle of " all or none." If a nerve cell is set into excitation at all, its excitation is *ipso facto* the greatest which is normally possible for it. A stimulus of the highest intensity can cause no greater response than can one of threshold intensity. The experimental demonstration of the validity of this principle for the individual nerve fibre has involved work of a very intricate and ingenious kind. But, on the theoretical side, it requires very little effort to see that the response of nervous tissue should be of the all-or-none type. If what the stimulus does is to upset the condition of semi-unstable equilibrium in the nerve membrane, the response of the nerve must depend upon its own inherent nature and not upon that of the stimulus. The old " train of gunpowder " analogy for the nerve impulse involved an all-or-none action, and the modern substitute for this classical mechanism makes the same theoretical demand.

Up to quite recently, it was supposed that a real exception to the all-or-none principle existed in the case of conduction through a section of nerve which had been narcotized, as by the action of alcohol vapor. The work of Adrian and Lucas[362] indicated that an impulse, in passing through such a narcotized stretch of fibre, decreased progressively in amplitude, the total decrease thus being proportional to the length of narcotized fibre through which it had passed. It was supposed that if the narcosis was sufficiently deep, or the length of the region sufficiently great, the reduction of the impulse amplitude could cause its complete extinction. If, however, the reduction did not carry the amplitude below a certain critical or threshold magnitude, the impulse, upon emerging from the narcotized stretch, would regain its normal amplitude and continue as if it had not passed through the narcotized region at all. But the recent work of Kato[363] shows quite convincingly that these interpretations of the observed phenomena were erroneous. It now appears that, although the amplitude of the impulse is reduced in a narcotized nerve, it does not suffer a decrement depending upon the length traversed; the amplitude is characteristic of the condition of the nerve at each point, just as in a normal fibre.

The evidence at hand points to the view that the action of a narcotic on a nerve cell is such as to produce a semipermanent increase in the permeability of the cell membrane, a physical state resembling that of refractory phase. Narcotics are apparently membrane destroyers, and the depth of the narcosis is represented physically by the extent to which the membrane has been chemically injured or made permeable. That this is a correct picture of the state of affairs in a narcotized region is indicated by the fact that such a region is electrically negative with respect to an unnarcotized portion of the nerve. It is also shown by observations that narcotic substances, such as alcohol, chloroform, and ether, increase the diffusion of materials through the cell boundaries. When an impulse encounters such a condition of the cell, its amplitude is correspondingly depressed, but if it is not extinguished altogether, it passes along until it reaches a healthy section and thereupon regains its full normal magnitude.

Although these facts corroborate the all-or-none principle, they make it evident that this principle cannot mean that all nerve impulses are of the same magnitude. The magnitude or amplitude of a nerve impulse depends upon the characteristics of the nerve substance in which it occurs, and not upon the character of the stimulus. This is the essence of the principle. The nerve characteristics differ for different nerve fibres in their normal conditions, and for the same fibre in various abnormal, subnormal or possibly supernormal states. They are probably different at synapses from what they are in the non-synaptic portions of the nerve. In a sense, the all-or-none principle simply formulates a thorough-going doctrine of specific nerve energies.

Davis, Forbes [364] and others point out that, although there is no conduction with a decrement in the previously accepted sense, there must be a so-called "transitional decrement," whenever an impulse passes from a region of higher to one of lower excitability. The amplitude of the impulse cannot change with complete abruptness, even if the excitability alters with position in this manner, since there must always be a certain amount of spreading of the forces belonging to one point into other regions. This is essential to the progressive excitatory effect which yields propagation. A similar "transitional increment" must exist when the impulse passes from a section of lower to one of higher excitability.

It is evident that the all-or-none principle, as applied to nerve activity, forces us to think of the latter in terms of fixed units of influence, so that we are faced by a system somewhat resembling that of the modern quantum theory of radiant energy. The nerve process is *quantal* or, to use a more biological term, for any given tissue, it is *isobolic.* The variations in the quantities of neural energy or influence which may be transmitted along a given nerve in unit time, must therefore be conceived to depend upon the number of impulses, or neural quanta, which pass through a cross-section of the nerve. This number is the nerve pulse frequency, and there cannot be the slightest doubt that the concept of such frequency is an absolutely basic one for the theory of nerve action, and hence for psychophysiology. However, we must not forget that the characteristics of a given nerve current are not completely determined by a specification of its frequency, since the amplitude, the length, and the form of the individual nerve pulse are independent of frequency, although they may serve to limit the latter.

236. Temporal Characteristics of Individual Nerves; Chronaxy. — The studies of Lapicque,[365] Erlanger, Gasser [366] and others have revealed some fundamentally significant temporal features of neural activity. It has been shown that each nerve and muscle cell has a characteristic speed, or inertia, of reaction. This can be measured by determining its *chronaxy,* which, according to Lapicque, is "the duration of action of a constant electrical current, instantaneously applied, which is required just to excite the cell, when the intensity of the current is double that which will just excite if infinite time is allowed." [367] The chronaxy of the gastrocnemius muscle of the frog lies between 0.3 and 0.5 σ.*

There are a number of other temporal aspects of the nerve process which stand in definite relationships to the chronaxy of the given cell. Thus, the shorter the chronaxial time, the more rapidly the impulse is conducted, the more rapidly does it develop at the point of excitation, and the briefer is the refractory period. The latent period and the summation interval for subliminal stimuli also are shorter, in general, for tissues which have a briefer chronaxy. Lapicque finds, in fact, that the chronaxy, τ, of a tissue can be employed as a unit of time in terms of which to measure its temporal characteristics and that when this is done all tissues follow approximately the same quantitative laws. Thus, the rate of rise of the excitation occupies a period equal to 2–3 τ while the time of decay or the refractory condition is 4–7 τ, and the total duration, $D = C\tau$, where C is a constant. Similarly, if V is the velocity of the impulse, $\tau V = K$, where K is a constant equal approximately to one centimeter. In other words, $V = K/\tau$, or one centimenter per chronaxial unit of time.

It has been shown by Lapicque and Legendre [368] that the chronaxy of a fibre is inversely proportional to its cross-sectional area; in other words, the larger the fibre, the more rapidly its processes occur. Now, it is an anatomical fact that the individual fibres which make up a single "nerve" may vary rather extensively in size. Consequently, we should expect that the rates of propagation of impulses in these fibres would vary, so that they would tend to get out of step with one another. The studies of Gasser and Erlanger[369] show that this is actually the case. The following table gives the velocities, in meters per second, for the various classes of fibres in a number of different nerves.

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* σ = one one-thousandth of a second.

TABLE V[370]

Preparation	*Temperature° C.*	*Velocity, Meters per second*			
		α	β	γ	δ
Bull frog sciatic	24.4	47.3	28.7	18.0	13.6
Bull frog sciatic	22.3	43.8	27.0	16.2	
Bull frog sciatic	21.0	41.3	25.6		
Green frog sciatic	23.3	33.3	17.0	9.4	
Dog Saphenous	38.0	83.3	57.8		
Dog tibial	38.0	80.4			
Dog vagus	38.0	53.6			
Dog phrenic	38.7	52.9			
Dog splanchnic	37.0	9.6			

The threshold is the lowest for the α class, increasing as the velocity decreases, a fact which makes it possible to stimulate the several classes, selectively. The absolute refractory period is 1.20 σ for the α class; 1.68 σ for the β class, and 3.13 σ for the γ class. However, in the case of the phrenic nerve of the dog, the refractory phase is as low as 0.6 σ.

It is evident that if a series of nerve impulses is aroused in a fibre, these must be separated by intervals of time greater than the duration of the absolute refractory period. Consequently, there is a limiting frequency for such impulses, which is given by the reciprocal of the absolute refractory period. For example, in the case of the phrenic of the dog, it would be 1666 per second. It is found that when one impulse follows another in the relative refractory phase of the first, the second impulse not only has a reduced amplitude, but travels more slowly, so that as it moves along the fibre, it tends to fall behind into a region of normal excitability. Hence there will be a tendency for the highest feasible frequency to be limited by the relative as well as by the absolute refractory phase. It has also been observed that a nerve is readily fatigued when it is excited at a rate higher than corresponds to the period of complete recovery.

237. The Basis of Nerve Current Strength. — Practically all so-called "nerves" consist of bundles of individual fibres, or axis cylinders. The smallest number found in any nerve is about ten (in a small cutaneous nerve of the frog, studied by Lucas); the largest (in the case of the human optic nerve), about a million. Some nerves apparently operate as functional units, whereas others may carry currents which are functionally differentiated. The phrenic nerve, which controls the contractions of the diaphragm in breathing, is in the former class, but a great many nerves carry both sensory and motor currents. We may also consider functional differentiation to exist when separate groups of fibres in the nerve carry impulses which yield introspectively separable components in experience. Thus, in the case of the human optic nerves, the excitations of different areas of the retina must be individually represented. The cutaneous nerves carry impulses which correspond with various modalities of sensation: pressure, warmth, cold, pain, etc. However, even where there is such a differentiation of function within a nerve, it is probable that there is a certain degree of coalescence of function between fibres which have closely adjacent receptoral connections, so that we may speak of functional conductive units which involve more than one fibre.

In the case of such a multifibral conducting unit, the strength or intensity of the nerve current may be regarded as consisting in the total number of quantal pulses which pass a given cross-section per second, regardless of whether the number is determined by impulse frequency in single fibres or by the number of co-acting fibres. The fact that nerves — and also, apparently, individual receptors in the same class — have different thresholds means that stimuli of low intensity will, in general, arouse fewer fibres than will those of higher intensity. If we accept the ideas of Hecht [371] on this subject, the number of fibres or receptors which have their thresholds within any given small range of intensities, can be represented as a function of the average intensity of this range, where the function in question has the general form of the probability integral. (See page 133, below.) At the same time, as shown by the studies of Adrian and Zotterman,[372] the number of pulses transmitted along the individual fibres may increase with the intensity of the stimulus. The strength of the nerve current, as thus conceived, bears a very close analogy to that of an electrical current, or a flux of radiant energy. In the former case, we are dealing with a stream of electrons, or ions, passing both in parallel and in series across a given section of the conductor. In the latter example, the light quanta stand in a similar relation to any unit of surface upon which the radiation may impinge.

238. The Mechanism of Receptor Cells. — Our account of the physical nature of nerve excitation and conduction needs to be supplemented by a discussion of the mechanism of the receptor. Receptors are recognized, in general, to be specially differentiated cells, often more epithelial than neural in character, which lower the threshold of a given nerve path for certain forms of influence, while raising it, at least relatively, for others. It is practically certain, moreover, that, in addition to being *stimulus selectors,* receptors are essential to the continued stimulation of nervous tissue by any agency which is not itself intermittent in action. Du Bois-Reymond's principle necessitates that the effect due to the direct action of any force upon the nerve should be a merely momentary one. In spite of the facts of sensory adaptation, stimulation through receptors must be acknowledged to yield relatively continuous excitation of the afferent nerve path. Sensory adaptation, itself, appears to be attributable mainly to fatigue of the receptor process rather than of the conductor.

I pointed out these relationships in an article[373] published thirteen years ago, and advocated a definite mechanism for meeting the theoretical requirements, in the case of visual response. It is only recently that the experimental studies of Adrian and his co-workers have definitely confirmed the general views expressed in this and a number of succeeding papers.[374] However, my conception of the process is still somewhat different from that which is advocated by Adrian.[375] We may begin with the assumption that the adequate stimulus to a bare nerve fibre consists in a change in electrical potential. When such a change is brought about by the application of a direct current voltage, ordinarily only one nerve impulse is generated, owing to the very rapid adaptation of the fibre to the action of the stimulus. If the latter is of very high intensity, two or three pulses may appear, but this will be the maximum possible number unless the voltage is varied. However, the facts of temporal sensation, together with the direct physiological measurements of Adrian, show that stimulation of a receptor cell produces a long series of impulses. It is therefore reasonable to suppose that the receptor operates somewhat after the fashion of an electrical interrupter, to apply an alternating or pulsatory series of potential variations to the nerve-end. It not only converts the specific stimulus force (*e.g.,* light, in the case of vision) into an electrical voltage, but automatically subjects this voltage to variations, such as can produce repeated excitation of the conductor.

The rapidity of this "buzzer action" must be supposed to be a function of the stimulus intensity which is affecting the receptor, the sensitivity of the latter, etc. Adrian's explanation of the process is as follows: The receptor cell adapts to the action of the stimulus very much less rapidly than does the conducting fibre, although the basis of its excitation is regarded as being essentially similar to that of the conductor. When excited, it goes into refractory phase, at the same time stimulating the fibre, which, however, completely recovers, so as to be ready for a second excitation, long before the receptor cell has become reëxcitable. But when the latter has recuperated, it is again set off by the stimulus and produces a second pulse in the nerve fibre, this process being continued with declining frequency of the impulses, due to the adaptation of the receptor. The rate of such adaptation varies with the identity of the species to which the receptor belongs; the so-called phasic receptors, like those of tickle, and thermal response, adapt very rapidly, while "postural" mechanisms, such as those of pain, lose their sensitivities slowly.

Now, it is evident that this general theory of the receptor process must be supplemented to explain how various non-electrical stimuli can cause excitation of the sensory cells, and to account for their different rates of adaptation. Owing to the wide variety of the stimuli in different sense departments, the exact mechanisms must be very different for different kinds of receptors. The extremely high sensitivity of certain receptors, such as the retinal rods, indicates a highly developed mechanism, possibly involving a number of stages, each of which is catalytically related to its predecessor. In general, it appears that the stimulus must act upon the receptor cell so as to bring about a threshold depolarization of the latter. In the case of vision, this might be due to the photoelectric liberation of electrons, which neutralize the layer of positive ions on the outside of the cells; in olfaction and taste, it may be referred to the chemical combination of the stimulus molecules with the membrane structure in such manner as to increase its permeability; or, in touch and audition, the permeability may suffer as a consequence of direct mechanical distortion.

239. **An Example of Receptor Action.** — As an illustration of a possible receptor mechanism, we may consider the view, previously mentioned, which I have advocated regarding the retinal response. This view is based upon the empirical finding that the retina is electrically negative, rather than positive as would be expected, with respect to the cut end of the optic nerve. Such negativity of the retina, which is increased by the action of light, seems to imply that the essential ionized substance of the rods and cones has a negative ion that diffuses through the enclosing membranes of the receptor cells more readily than does the positive ion, producing a state of polarization opposite in direction to

that of ordinary nerve fibre. It is clear that a receptor cell, thus polarized and in contact with a normal nerve fibre, would tend to depolarize the latter at the place of junction, and hence set the fibre into excitation. The excitation would probably be mutual, resulting in a reduction of the polarization both of the nerve membrane and of the receptor membrane. We have reasons for supposing that the inertia of the visual receptor process is much greater than that of the optic nerve function, so that, in all probability, the nerve would recover from refractory phase considerably in advance of the recuperation of the receptor cell polarization. However, when this latter recuperation has reached a certain point, a second stimulation of the nerve fibre will result and this process will be indefinitely repeated. The result will be a stream of quantal impulses, sent along the optic nerve fibres, having a frequency determined by the rate of recuperation of the receptor cell.

In the visual response it is easy to see how this frequency can be caused to vary as a result of variations in the stimulus. The direct effect of light upon the sensitive substance of the rods or cones is probably one of increased ionization and we should expect the rate of repolarization of the receptor cell membrane to increase with increase in concentration of the ions within the cell. The optic nerve impulse frequency would thus tend to be augmented by the action of radiation on the retina, and to a degree greater the intensity of the radiation of any given wave-length. The number of pulses per second would also vary as a function of the spectral absorption curve of the photochemical substance, and with the concentration of the latter at any time. When the ionization and activity of the cell is increased by stimulation, this substance will tend to be depleted, thus causing a reduction in the degree of the response, for constant objective conditions, as time goes on. This is the essential basis of the sensory adaptation. Recovery, after the stimulus has been removed or reduced, is naturally attributable to the restitution of the photochemical substance. (*Cf.* page 123, below.)

It is not necessary to suppose that all receptor cells are characterized by the possession of negative polarization, although this may be a common property of those which exhibit automatic activity, or self-excitation. Rhythmic depolarization mechanisms of this nature may also exist in the central nervous system, and be affected in their rate of discharge by the chemical constitution of the blood stream. The operation of the breathing center, and other central mechanisms, such as those determining certain types of peristaltic action and muscle tonus, may have this basis.

240. The Special Properties of Synapses. — Facts summarized in a masterly way by Sherrington[376] show that nerve conduction through a complete reflex arc differs radically from conduction between two points in a single nerve fibre. This difference is attributable not only to the peculiarities of the receptors but also to those of the *synapses,* or junction points between the individual neurones in the conducting series. Although synapses are especially characteristic of the nerve centers, they are also involved in the majority of afferent paths.

The differences between synapses and normal conducting nerve tissue, as signalized by Sherrington, in his classical list, are as follows: (1) slow speed of response, especially in the form of a prolonged initial delay (latent period), (2) extensive after-discharge, (3) lack of correspondence of rhythm of stimulus and effect, (4) lack of correspondence between the intensity gradations of stimulus and effect, (5) resistance to a single stimulus, combined with a summation of the effects of successive small stimuli, (6) conduction only from afferent to efferent, (7) relatively great fatigability, (8) relatively great general variability of the threshold, (9) very long refractory periods, (10) great dependency upon oxygen and (11) relatively great susceptibility to the action of drugs. These characteristics are nearly all consistent with the generalization that the synapse exhibits more inertia in its response than does a continuous single nerve fibre or a group of such fibres, operating in parallel. We cannot be sure that all of these properties belong exclusively to the synapses, since other structures — such as the cell-body — may contribute to the peculiarities of reflex, as opposed to nerve trunk, conduction.

The simplest way in which to conceive of the physiological specialization of the synapse is to regard it as a region of depressed excitability, similar to that which can be produced by local application of a narcotic. When a nerve impulse arrives at such a region its amplitude is reduced, and it may even disappear completely, depending upon the magnitude of the impulse and the depth of the narcosis. It has been shown experimentally that impulses which have been aroused in relative refractory phase, and hence have a subnormal intensity, may fail to traverse a narcotized section of nerve, even if normal impulses succeed in getting through. The normal impulses are reduced in amplitude while in the region of narcosis, but regain their normal sizes if they emerge at all. It is not necessary to assume that there is conduction with a decrement either in the narcotized stretch or in the synapse, in order to account for these results. Nevertheless, as pointed out by Forbes and his associates, there must actually be a certain amount of conduction of this sort across the boundary line between nerve sectors which are of unequal responsivity. (See page 37, above.)

All of the evidence at hand points to the view that the action of a narcotic on a nerve cell consists essentially in a persistent increase of the permeability of the cell membrane, a state physically resembling that of refractory phase. Narcotics are apparently membrane destroyers, and the depth of the narcosis represents the degree to which the membrane has been injured or made permeable. That this is the correct picture of the state of affairs in a narcotized region, is indicated by the fact that such a region is electrically negative with respect to an unnarcotized portion of the nerve. It is also corroborated by the observation already noted, that narcotic substances increase the diffusion of materials through cell boundaries. The depression of the impulse amplitude under such conditions is readily understood, since the process of excitation consists in the change from a condition of low to one of high permeability. If the permeability is already comparatively high, the possible range of the process is obviously reduced.

Now, it is possible to predict the existence of a state of this sort at a synapse, on the basis of assumptions which have already been made. We have defined a synapse as a point of contact or proximity between two neurones. In accordance with the Nernst-Lillie theory, each of these neurones, in the state of rest, bears a layer of positive ions upon its surface. Consequently, each neurone will act upon the other as if it were an anode, and should be expected to induce in its neighbor a condition of anelectrotonus, which — as we have seen — involves an increased permeability of the membrane and reduced excitability. The anelectrotonic state will be restricted to the zone of contact of the two neurones and should be shared by them both. The local reduction in the impermeability of the membrane may be attributed to the compensatory adjustment of the latter to the presence of two intermingling layers of positive ions. The two cells assist each other in maintaining the external potential and hence each one can reduce its contribution of ionic selection.

241. Special Processes at Synapses. — When an impulse arrives at such a synapse, the local reduction in the positivity of the membrane surface, or interface, should be approximately half that which characterizes other portions of the cell, since the contribution which is made by the adjoining cell will, in the first instance, be unaffected. However, the change which actually does take place will be effective upon the second cell as a stimulus, since it constitutes a partial depolarization of its surface. Whether or not this will be sufficient to cause excitation must depend upon the condition and normal excitability of the second cell. The synaptic process is evidently more complicated than that of plain conduction, since it involves the combined properties of two membranes in juxtaposition. Some of the peculiar characteristics of conduction through synapses, which may not be explicable by the supposition of mere quantitative differences in excitability and response between the synapse and the nerve fibre, may perhaps be accounted for on the basis of differences between the two membrane elements which are always involved. Thus, the fact that a synapse normally conducts in only one direction can be attributed to a difference between the amplitudes and thresholds of excitation for the two adjoining neurones, such that the more afferent neurone is able to stimulate a more efferent one, but not *vice versa.* The first cell might have a relatively high amplitude and low excitability, while the second has a low amplitude and high excitability.

According to the views of Lapicque [377] and his collaborators, the operations at synapses are largely dependent upon chronaxial relations between the impinging conductors. If the inleading and outleading conductors have nearly the same chronaxy, or are *isochronous,* the excitation is passed through the synapse efficiently. However, if the ratio of the two chronaxies is greater than about two to one, there can be no transmission. Lesser degrees of *heterochronism* stand for various amounts of resistance to the passage of the nerve current. Lapicque finds that motor nerves and their attached muscle-cells are isochronous, and that transmission from nerve to muscle through the so-called end-plate depends upon this condition. Alkaloids, such as curare, which interfere with such transmission, do so by throwing the elements out of synchronism, either by raising or lowering their chronaxies differently. This view makes it unnecessary to postulate the existence of a specific end-plate tissue, supposedly influenced specifically by (*e.g.*) curare. Similar alterations in chronaxial relationship may occur in synapses, either in consequence of the presence of drugs and fatigue substances or of processes of learning.

Lapicque [378] finds that transmission across central synapses (as in the spinal cord) is not strictly isochronous, but may involve auxiliary processes of summation. Certain motor functions have the property of requiring a *series* of stimuli, properly timed, in order to set them into excitation, not being excitable by a single stimulus, no matter how intense the latter may be. According to Lapicque, this *iterative* character is to be assigned to the internuncial neurones of the centers, so that a series of relatively rapid impulses is required of the sensory fibre in order to set off the slower tempo of the central and efferent process. These relationships can be represented by means of a definite mathematical formula.

However, synapses are not merely points at which nerve currents are passed from one neurone to another, or at which they may be blocked on account of structurally conditioned resistances. They are also loci of interaction between currents which arrive simultaneously along separate neural channels. In this way, they furnish the indispensable means for the formation of dynamical nerve networks, and make possible "the integrative action of the nervous system." Now, the fundamental modes of interaction between concurrent nerve processes appear to be *summation* and *interference;* they may either assist one another in producing a single type of effect or certain of them may be *inhibited* by others. Authorities differ regarding the exact manner in which these processes are best explained. According to one view, they can be understood in terms of the general principles of nerve action, which we have already outlined. It seems more probable, however, that the nerve centers contain many special mechanisms, in addition to those of plain conducting tissue, or of the synapse considered merely as a region of reduced excitability.

Adrian endeavored to account for certain phenomena of summation in terms of the supposed increase in amplitude of nerve impulses set off during the alleged phase of hyperexcitability, but this now seems to be definitely excluded from the domain of normal nervous activity. However, Adrian's related explanation of inhibition can still be considered applicable to certain cases of neural interference. If a nerve is stimulated at a rate which is in excess of its ability to recover from refractory phase, it tends to stay continuously in this latter condition. If impulses are generated, subsequently to the first one, they are of low amplitude. Now, if a high frequency nerve current impinges upon a synapse or synaptic region which is relatively slow in recovering from the refractory condition, the result should be that the synapse in question is maintained in an inexcitable state as long as the current continues. Other currents, of lower frequency, will thus be prevented from passing through. This kind of interference can readily be demonstrated experimentally in a nerve-muscle preparation, where it is known as Wedensky inhibition.

A close study of the facts of summation and inhibition indicates, however, that factors are probably involved which are quite different from those essential to nerve fibre excitation. Sherrington and others[379] favor the view that excitation in nerve centers involves the accumulation of a state or substance, designated as *E,* which is non-quantal and has no refractory phase. Each nerve impulse arriving at a center liberates a quantity of *E,* and the concentration of the latter increases during a succession of impulses, although this increase is opposed by a process of dissipation. Efferent impulses are set up in the usual pulsatory form, but at a frequency which is determined by the concomitant value of *E,* rather than by the temporal pattern of the afferent currents. *E* thus operates very much like the concentration of the supposed photochemical end-products in the retinal receptors. Inhibition, in accordance with this type of theory, involves a second condition or substance, *I,* which is also cumulative, but which is capable of neutralizing equivalent amounts of *E. I* is released in the centers by the action of specific inhibitory nerve terminations. Although *E* and *I* are undoubtedly operative upon the synapses, their production probably involves the activity of the nerve-cell bodies.

We shall have a great deal more to say concerning the probable details of central nerve processes in our chapters dealing with cerebration, where these processes as they are exemplified in the cerebral cortex will represent our primary interest. For the present, our concern is with stimuli, receptor activities and afferent nerve currents in their relationships to experience.

Chapter XIV

Visual Sensation

242. General Analysis of the Problem. — In accordance with our general concept of sensation, we must define visual sensation so as to involve the relationships between experience, on the one hand, and the visual stimulus, ocular and optic nerve processes, on the other hand. On account of the fact that the rays of radiant energy which enter the eyes may stretch continuously from far distant objects to the retina, it is necessary to establish an arbitrary line of demarcation which will serve to separate the objective from the "afferent arc" phases of the response process. This boundary may conveniently be placed at the surface of the cornea, where the rays leave the air and enter the living substance. It is evident that only those rays, which are not absorbed by any of the ocular media, can actually constitute visual stimuli. We have already considered, in our chapter on visual perception, the most important and characteristic relationships which hold between visual experience and various aspects of the objective phase of the response process.

The intraocular process can be divided into a number of distinct stages, but the most general subdivisions are (1) the refractive, and (2) the retinal. The former include the successive bendings of the rays at the surfaces of the cornea, the aqueous humor, the crystalline lens, and the vitreous humor. Certain other significant modifications of the rays also occur within these media; they are partially absorbed and scattered in characteristic ways. The retinal stage is also complex, but its essential feature comprises the visual receptor process. Following this, we must consider the manner in which the excitation is transferred to the optic nerve fibres, and the mechanism of its transmission along the latter to the brain. Our primary problem is, of course, to establish the psychophysiological relationships which exist between visual experience and each of these successive stages in the afferent arc mechanism.

The general topic of visual sensation may be divided, first, into the *monocular* and the *binocular* departments. Under each of these categories, we can distinguish between component, composite, and temporally conditioned sensation. The first relates to the physiological conditions, within the afferent arc, for *elementary* subjective impressions, such as points of color or of depth. The second is concerned with spatial patterns, presenting a plurality of such points, simultaneously, while the third deals with changes. Classical psychologies have tended to restrict the study of visual sensation to component monocular variables, the understanding of which is practically equivalent to the science of "color vision," in its broadest aspects. However, our own definition of sensation compels us to consider as sensory any relationship which can be established between experience and factors contained in the afferent arc. Such relationships may involve the binocular as well as a monocular system. Spatial configurations must be considered in addition to the parts which enter into their composition.

Some difficulties are encountered in endeavoring to draw sharp lines of demarcation between component, composite, and temporal sensations. Ideally, we might study the psychophysiology of color for a single point in visual space, in relation to only one retinal receptor with its associated stimuli and nerve conduction lines. In practice, however, we always have to deal with some definite pattern, in experience, and with a group of functionally interdependent factors on the physiological side. Nevertheless, it is still possible to make a logical separation of the three aspects, and, as in the case of perception, we shall base this upon introspective criteria. An introspective component may sometimes depend for its nature upon physiological *patterns* or *processes*, but this does not prevent us from treating it as a component, and as static. Thus, our treatment of color as a component of visual experience may legitimately include a discussion of its determination by such physiological factors as position, pattern, contrast, stimulus duration, etc. However, if the *pattern* of visual experience, itself, is definitely before us as a dependent variable, we are dealing with problems in composite sensation. If subjective visual *changes*, as such, are being considered, the problem is one in temporal sensation.

However, for practical reasons, we shall not attempt to adhere strictly to the logical schema just indicated. The distinction between component, composite, and temporal aspects has been sufficiently emphasized in the treatment of perceptual problems. The majority of the principles which are involved under these categories, in the study of sensation, are rather obvious deductions from those considered for perception. The main subdivisions of visual sensation can most profitably be made along different lines, particularly that between achromatic and chromatic response. We shall therefore treat the composite and temporal features of visual sensation along with the component, in the most convenient contexts, without insisting upon their strictly logical separation.

243. The Principal Aspects of Color Sensation. — The problems of component monocular sensation are confined almost entirely to relationships between *color* and various factors in the afferent arc process which determine its varieties in experience. We must recall that the term, color, has been defined so as to include black, white and grays, as well as qualities which exhibit the attribute of hue. (See Volume I, pages 246–254 or Note A, page 351, this volume.) We have distinguished between the gray series of colors, as achromatic, and the hued group, as chromatic. We have seen that all possible colors can be arranged into a three dimensional system, the color solid, so that the character of any color can be specified in terms of three attributes: brilliance, hue and saturation. The attribute called brilliance is the essential determinant of the achromatic series of colors, ranging from zero at an ideal black to a maximal value at "white." However, brilliance also enters into the constitution of chromatic colors, which have the additional features of hue and saturation. Hue indicates the mode of variation of color, according to which it is reddish, yellowish, greenish or bluish; and saturation is a sort of measure of "amount of hue," or "hueness."

The simplest view concerning the psychophysical relationships of color envisages a correlation of brilliance, hue and saturation with intensity, wave-length and degree of homogeneity, respectively, in the stimulus. However, even the most cursory scientific study shows that no such simple set of relationships actually holds. Each of the color attributes is determined in an important way by practically all of the stimulus characteristics, as well as by features of the sense-organ and receptor stages. The problem which is before us is evidently that of ascertaining the functional relationships, or laws, which link each of the three attributes of color with afferent-arc variables. One way of studying such functions would be to determine the loci, in the color solid (see page 354), of the colors which are elicited by all values of any single independently variable factor on the physiological side, when other factors are held constant. This represents the usual method of experimentation. For purposes of exposition, however, it is better to consider each of the three attributes separately, in relation to each important variable on the physical side. Other variables will be regarded as constant, except when we desire to see how a given psychophysical function changes when its conditions are altered. Thus, we may investigate the manner in which brilliance depends upon wave-length, and how the form of the law connecting the two is itself affected by intensity, states of retinal adaptation, etc.

The attributes of hue and saturation show a closer relationship to each other than they do to brilliance. The latter is primarily characteristic of the system of achromatic colors, which seem to be the most primitive kinds of color experience, and to form a sort of framework upon which the chromatic colors are supported. Consequently, we can profitably divide our discussion so as to consider, first, the psychophysiology of brilliance and then the added facts relating to hue and saturation. We shall begin with a brief discussion of the nature of the visual stimulus. Then we shall consider the laws connecting brilliance with stimulus characteristics. Following this, we shall deal with its intraocular and retinal correlations, and finally, we shall treat of the relationships between brilliance and the processes of the optic nerves. It will aid in this discussion to have the facts of composite and temporal sensation before us, insofar as they involve brilliance. The attributes of hue and saturation will be treated in accordance with the same general plan.

244. **The Problem of Binocular Sensation.** — Binocular sensory problems will be discussed only briefly, since we have already treated the best established principles of binocular vision in our study of visual perception. However, perception — as we have defined it — excludes all afferent arc factors, and these are definitely concerned in the binocular process. Hence, there must be a science of *binocular sensation,* which is concerned with the manner in which experience varies as a function of the relationship between the right and left eye afferent systems. The theory of corresponding rays must be translated into one of corresponding retinal points. The relationships obtaining between depth impression and retinal disparation must be studied, together with other peculiarities of binocular vision, such as Fechner's paradox and the "reflexive" fatigue effects demonstrated by Frank Allen. (See pages 202–205, below.)

Section 53

THE NATURE OF THE VISUAL STIMULUS

245. **Light and Radiant Energy.** — Although vision is classed as a "distance receptive" sense, responding to objects outside of the eye, we must recognize that the actual

visual stimulus is the *retinal image,* a pattern of radiant energy impinging upon the most sensitive tissues of the eye itself. Contact of this radiant energy with the rods and cones — the visual receptors — is just as essential to visual response as is the mechanical contact of objects with the skin in touch. It is commonly stated that the adequate visual stimulus consists of "light," and this statement can be accepted, if accompanied by a proper understanding of the modern interpretation of photometric concepts. As we shall see (*cf.* page 71), the term, light, is no longer used technically as an equivalent of radiant energy, whether or not the latter is "visible." Light consists in radiant energy evaluated in terms of its capacity for evoking brilliance, when it acts upon an "average normal" psychophysiological organism. Consequently, if we are interested to formulate psychophysical laws which have exclusively physical terms on one side of the equation, we must avoid the photometric concepts and use those of radiant energy, pure and simple.

However, a physical agency becomes a stimulus only by virtue of its power to stimulate, so that the concept of light can legitimately be employed if we keep constantly in mind the exact manner in which it is defined. It turns out that the use of photometric measures enables us to simplify the formulation of the majority of visual psychophysical laws. Nevertheless, the first step in our analysis must involve a clear understanding of the facts upon which the notion of light is founded, and this necessitates that we should consider the manner in which brilliance is determined by purely radiometric or energy factors. Light values are derived from such purely objective quantities by applying coefficients which represent the relative brilliance-producing capacities of various kinds of radiant energy.

Radiant energy, or "radiation," as it is sometimes called by way of abbreviation, is a form of wave motion which travels through empty space at the astounding rate of 186,000 miles a second. These waves were formerly said to be undulations in a cosmic fluid called the ether, but the physical reality of the latter has been rendered doubtful by modern considerations, summarized in Einstein's theory of relativity. It is definitely established, however, that radiant energy consists in propagated oscillations in the intensities of electric and magnetic fields, which exist in the space through which radiant energy travels. In the present state of physical thought it seems best to replace the ether by the so-called "lines of force"[380] which are employed in physical diagrams to represent such fields, especially the electric field. Following the scheme first suggested by Benjamin Franklin, every electric charge is conceived to have attached to it a certain number of unit force lines as shown in Fig. 33. When such an electric charge is disturbed, either from a state of rest or of uniform motion, waves are produced

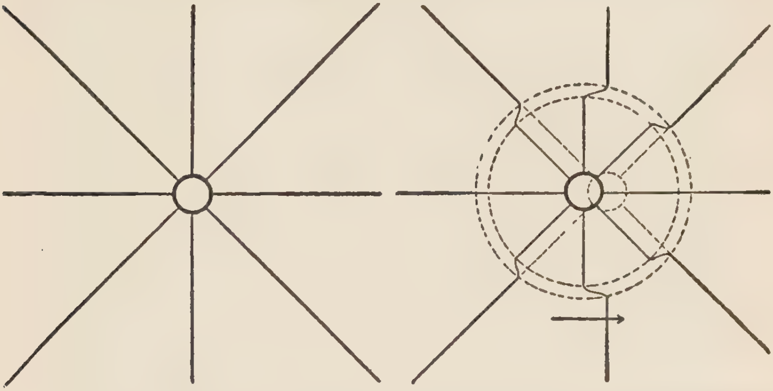


Fig. 33. To Show How Radiation Is Produced by Stopping the Motion of an Electrical Particle.

The diagram at the left represents a charge of electricity with its radiating lines of forces. We will suppose this charge with its lines to be moving uniformly in the direction indicated by the arrow in the diagram at the right. When the charge is suddenly brought to rest the "lines" have a tendency to continue in motion, and do so until, so to speak, the news of the stopping of the charge has reached them. This "news" travels outwards from the charge with the velocity of light, along with the "kinks" in the force-lines which result from the discrepancy between the actual and the "expected" position of the charge. These kinks contain electro-magnetic energy and constitute light and other forms of electro-magnetic radiation. Such radiation is produced whenever any change whatsoever occurs in the state of uniform motion of an electrical charge.

in its lines of force, much as they can be generated in a rope under tension which is shaken at one end. Owing to the excessive tension of the force lines, these waves travel away from the charge at the tremendous velocity just specified.

It was formerly supposed that ordinary radiation involves a continuous series of such undulations in the electric force lines and that the amplitude of these undulations falls off continuously as they travel away from their sources. However, the modern quantum theory of radiation affirms that the radiation takes place more or less discontinuously, in the form of relatively short trains of waves and that these wave trains travel along a restricted path without losing amplitude, the apparent loss of intensity with distance being due to a reduction in the total number of such trains striking a given surface. Although this quantum notion confers upon radiant energy some of the properties of material particles, it is by no means a return to the old and rejected corpuscular theory of Newton.

246. The Three Characteristics of Radiant Energy. — Any given sample of radiant energy possesses three general characteristics which are of importance in its operation as a visual stimulus. The most fundamental of these is that of wave-length, which is the distance measured in any convenient unit from one wave crest to the next adjacent crest. It is conceivable that electromagnetic waves should have any possible vibrational form, but, as they are presented in the spectrum, we regard them as sinusoidal or as following the law of simple harmonic motion. Waves having a more complex contour could be analyzed mathematically, or by the spectroscope, into a group of sinusoidal waves of different lengths and amplitudes. Any sample of radiant energy which, under such analysis, proves to be substantially of a simple wave-length is described as *homogeneous,* or sometimes as *monochromatic,* although this latter term is not to be recommended on account of its psychological connotations. Radiant energy which proves upon analysis to be complex is called *heterogeneous.* Practically all of the radiant energy that is involved in ordinary visual stimulation is highly heterogeneous. Only under carefully arranged conditions of laboratory experimentation, do we have to deal with the effects of homogeneous radiation.

The second important characteristic of radiant energy is that of intensity. Intensity corresponds roughly to the amplitude of the waves, although on the quantum theory it also involves the *number* of simultaneously effective wave trains. Moreover, as ordinarily measured, the intensity is proportional to the energy of the waves, and this in turn depends upon the square of the amplitude and the reciprocal of the wave-length. Because of these complications, it seems advisable not to try to *picture* the nature of intensity, although it is much easier to measure intensity than amplitude. Intensity is always proportional to the rate at which energy flows into a given surface, and this rate can readily be measured by the heating effects which are produced. The intensity of the retinal stimulus is also expressible in terms of such a rate of energy flow.

Any sample of homogeneous radiant energy can be characterized perfectly by specifying its single wave-length and its intensity. In the case of heterogeneous radiant energy, however, this must be done separately for each different represented wave-length. In certain instances, as in so-called "line spectra," there is a limited number of these component wave-lengths, so that the complete constitution of the sample can be represented by means of a *table* of wave-lengths and intensities. However, in by far the commonest case, there is an infinite number of wave-lengths, or the spectrum is *continuous*. In such cases, it is necessary to represent the constitution of the radiation by means of a *graph*, in which intensity is plotted against wave-length, or by means of an equation which gives the intensity as a function of the wave-length. Graphs of this sort are called intensity distribution curves, examples of which are shown in Fig. 34. They constitute the best method for specifying the total nature of complex samples of radiant energy. The form of such a distribution comprises the third general characteristic of the visual stimulus: its *wave-length composition.*

247. Measures of Wave-Length. — In order to plot a distribution curve, it is necessary to have definite units in terms of which to measure both wave-lengths and intensities. The former can of course be expressed by using any unit of length, but in the case of visible radiation, on account of the very small distances that are involved, the unit usually employed is the millimicron, one millionth of a millimeter. This unit is properly symbolized by the letters, $m\mu$. Physicists have demonstrated the possibility and the existence of electromagnetic waves, varying in length from less than 1/1000 of a millimicron to more than 400 billion of these units. The shortest known waves are the " cosmic rays " of Millikan; then come those emitted by radio-active substances and known as gamma rays; next in order follow the X-rays, which are of the order of magnitude of 1/100 millimicron in length. The so-called ultra-violet rays range from approximately 20 millimicrons to 400 millimicrons,[381] the latter value corresponding roughly with the beginning of the visible spectrum.

Visible radiant energy, commonly called " light," extends from approximately 400 to approximately 760 millimicrons. Higher wave-lengths include the so-called infrared rays, up to a value of about 300,000 millimicrons, and finally the Hertzian waves, employed in radio communication or broadcasting, and having, for example, a length of 400 meters or 400 billion millimicrons. It is evident that only a very small portion of the enormous existing range of wave-lengths is capable of influencing the eye; in fact, if a normal spectrum containing all visible radiations and one yard long (similar to the chart used in laboratories) were extended proportionately to include all known waves it would become about 5 million miles in length. The only essential differences between the various classes of radiant energy lie in their wave-length characteristics, so that invisibility is due to the properties of the eye, rather than to those of radiant energy *per se.* It must be recognized, however, that the peculiar sensibility of the eye to waves lying between 400 and 760 $m\mu$ is based, evolutionarily, upon the physical fact that, within this range, the radiant energy coming to us from the sun finds its maximal intensity.

Purity. — It is sometimes convenient to have an expression for the relative homogeneity of any given sample of radiant energy, which does not involve the complete form of the distribution curve, but represents its general characteristics by means of an average. This is provided in the concept of *purity,* which can be defined, with respect to any selected constituent of the given sample, as the ratio of the intensity of this constituent to the total intensity of the sample. Such intensity can be measured radiometrically, photometrically or colorimetrically, thus yielding three separate purity concepts. Only the first of these is purely physical in its significance. Reference should be had to the *Report of the Committee on Colorimetry of the Optical Society of America,* for the year 1920–21 for further discussion of these ideas.

248. Radiometric and Photometric Intensity Measures. — Intensities can be measured either radiometrically or photometrically, and the results of these two methods should never be confused. They are related by a simple multiplicative coefficient for stimuli of fixed wave-length composition, but are expressed in different units. Radiant intensity is measured in ergs per second, in watts or some other unit of *power* (rate of transfer of energy). Instruments for making such measurements are called radiometers, and usually involve an electrical detection of the amount of heat that is produced by the absorption of the radiant energy stream.[382] Measurements of light intensity are made with a photometer, and require the eye or some device, such as a photoelectric cell, which has been calibrated in terms of the eye.

The commonest *photometric* measures[383] are those of *illumination* and *brightness,* respectively. *Illumination* is expressed in terms of meter-candles or foot-candles, the flow of light through a surface at a distance of one meter or one foot, respectively, from a standard candle. The amount of light-flow in a unit solid angle, with its center at the candle, is known as a *lumen;* it is the total light striking a surface of one square meter area at a distance of one meter from the candle. *Brightness* is a measure of the *candle-power per unit area* of a surface which is regarded as a source of light, and represents the lumens emitted, in a given direction, per unit area per unit solid angle. It may be expressed in candles per square meter or in millilamberts. Illumination and brightness have definite analogues in radiometry. Thus, illumination corresponds to a measure of the density of energy-flow into a surface, which can be specified in ergs per second per square centimeter. The analogue of brightness consists in the number of ergs emitted or reflected from a unit of surface within a unit solid angle.

As we have seen, the true physiological stimulus to vision is the retinal image. However, in practice, we are unable to measure the characteristics of this image directly, although they can be computed with a considerable degree of accuracy. In the vast majority of experimental studies in visual psychophysiology, we are compelled to specify the stimulus in objective terms. Nevertheless, we should select these terms so that they will be maximally significant with respect to the stimulus value of the retinal image. To this end, I have proposed and have used in my own researches, a unit of intensity called the *photon.*[384] This unit takes into consideration the fact that the intensity of the retinal image, and hence of the effective visual stimulus, depends upon the area of the pupil of the eye combined with the photometric brightness of the object surface, viewed from the eye position. Accordingly, the photon is defined as the intensity which accompanies the use of an object brightness of one candle per square meter and an externally effective pupillary area of one square millimeter. The photon value is said to measure the *physiological intensity* of the visual stimulus, and it can be computed approximately by multiplying the brightness measure by the area of the pupil in square millimeters. It is proportional to the *illumination* of the corresponding portion of the retinal image. If it is desired to replace the photometric measure by its radiometric analogue, we need only to divide the photon value by the visibility coefficient of the kind of radiant energy which is involved in the given instance. We shall explain the relationships between radiometric, photometric and visibility concepts in greater detail below. (See pages 68–70.)

When we speak of "intensity" in the following pages, without qualification as a characteristic of the visual stimulus, it should be interpreted in terms of the photon or its radiometric analogue.

249. Distribution Curves of Common Radiant Sources. — As we have seen in our discussion of visual perception, a complete understanding of the psychophysics of color demands a consideration of several stages of transformation of the radiant energy, prior to its incidence upon the retina. One must consider, in the first place, the characteristics of the "source." The distribution curves for the most common sources of visible radiation are of a type called by physicists "black body" curves. A family of these curves (shown in Fig. 34) may be chosen so as to represent quite accurately the distributions of such common sources as (1) sunlight, (2) the carbon arc, (3) the various tungsten lamps, whether gas-filled or vacuum, (4) the carbon incandescent lamp, (5) kerosene or gas flame, or (6) even the candle.

All of these curves can be derived from a single equation known as Planck's law, by substituting in the equation for this law various values representative of different temperatures. The higher the temperature, the farther the maximum or single hump of the curve lies towards the shorter wave-lengths, and the greater the area which the curve includes. Fig. 34 shows only the parts of the given curves falling within the visible spectrum. Such black body curves represent maximally non-selective radiation, the characteristics of which are determined by temperature only and not by the nature of the radiating bodies. Other sources, such as the mercury arc, the cerium and other impregnated arcs,

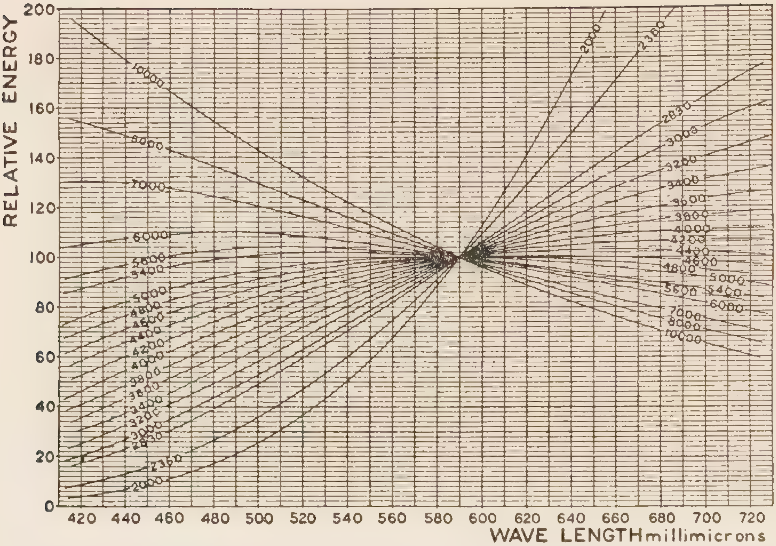


Fig. 34. Curves Showing Black Body Intensity Distributions at Various Temperatures.

The above distribution curves were computed from the formula of Planck, using a value of Planck's constant, $c_2 = 14350$ micron degrees. The numbers attached to the individual curves indicate temperatures in degrees, Kelvin. Characteristic (color-) temperatures of common light sources are as follows: (1) sunlight, 5200°, (2) carbon arc, 3780°, (3) Mazda B tungsten incandescent lamp, 2385°, (4) carbon incandescent lamp, 2070°, (5) kerosene lamp, 1915°, and (6) paraffin candle, 1920°.

the Welsbach mantel, etc., have less regular curves, depending upon the special character of the incandescent substances which are involved.

250. Aspects of Reflection and Transmission. — Radiant energy, before reaching the eye, is ordinarily reflected or transmitted by some material medium which, in general, modifies the distribution curve. The exact natures of these modifications are characteristic of the objects that reflect or transmit the radiant energy, and thus carry information concerning such objects. Objects which we call "white," or neutral, reduce all of the ordinates of a distribution curve proportionally, so that the relative distribution remains unchanged, the total amount of energy varying from a high percentage for white to a low percentage for so-called "black" objects. The objects which we call "colored" reflect or transmit different wave-lengths to different degrees. They are said to be *selectively absorptive.* "Colored objects" are always darker than are "white" objects, even when the former are of maximal brightness, because of the fact that the modification of the distribution curves involves a *subtraction* of intensity at some wave-lengths, and never an addition (except in the case of secondary radiation, phosphorescent or fluorescent). The change in the distribution curve of the radiation which results from reflection or transmission by a selectively absorptive object

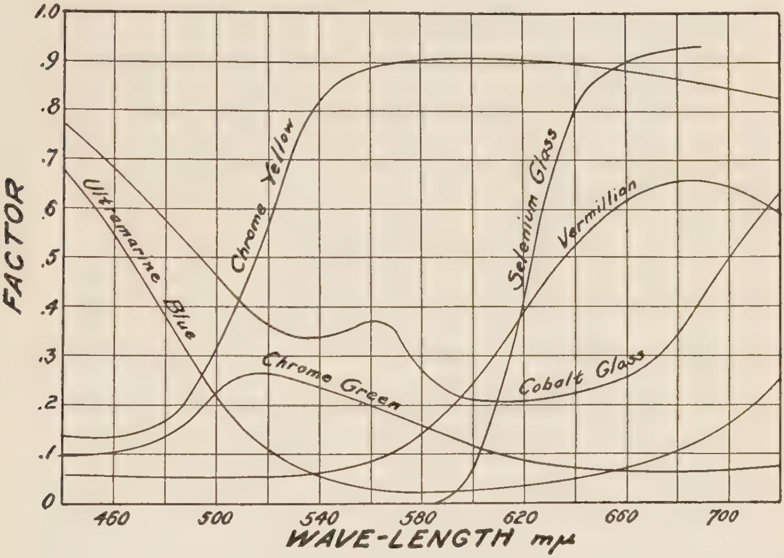


FIG. 35. CURVES SHOWING SPECTRAL REFLECTION AND TRANSMISSION CHARACTERISTICS OF VARIOUS SUBSTANCES.

In the case of the paint pigments, names of which are given on the curves, the fraction of light reflected is shown for each wave-length. In the case of the selenium and cobalt glasses, the fraction of light which is transmitted is given. In order to obtain the distribution of intensity among different wave-lengths for the radiant energy reflected or transmitted by any substance, the value of the fraction at each wave-length must be multiplied by the source intensity at the same wave-length (see Fig. 34).

can be predicted from its spectral reflection or transmission curve. Examples of such curves for common pigments are given in Fig. 35.

It should be borne in mind in connection with these considerations that there is no absolutely fixed standard of "whiteness," or lack of "color," in a source of radiant energy. The natural standard is probably noon daylight, or a combination of solar radiation with scattered rays from the atmosphere. This combination corresponds approximately to a black-body distribution at a color temperature between 5200° and 5800° Kelvin. However, considerable deviations from this type of distribution can occur without seriously upsetting our impression of neutral illumination, or of the color relationships of objects.

Section 54

MONOCULAR STIMULUS RELATIONSHIPS INVOLVING BRILLIANCE

I. Brilliance as a Function of Wave-Length

251. The Direct Psychophysical Function. — Although we ordinarily regard brilliance as the representation of intensity, its dependency upon wave-length is even more fundamental. However, in order to demonstrate this fact, we must experiment, at different wave-lengths, with intensities which are radiometrically rather than photometrically equal, since the concept of light has already discounted the relative capacities of different kinds of radiant energy to produce vision. Proceeding in this manner, we may determine the brilliance values, on a scale of just noticeably different degrees of this attribute, which accompany stimuli differing in wave-length. Determinations of this kind have apparently not been made experimentally, but the general nature of the relationship can be computed from available data. The resulting function, as represented in Fig. 36, shows a single maximum in the same position as that of the corresponding visibility curve, but differs from the latter in the absence of

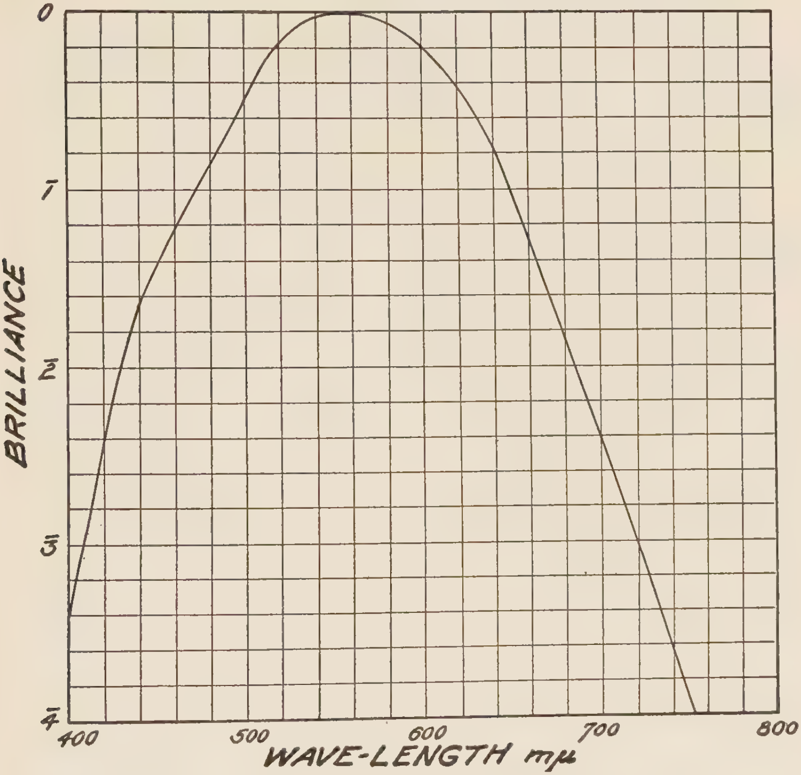


Fig. 36. Brilliance as a Function of Wave-Length.

This curve is intended to show how brilliance would vary as a function of wave-length with equal radiant intensities at all wave-lengths. The curve was derived from the visibility data of the Optical Society of America, by plotting the logarithms of the visibility coefficients in place of the latter directly. It assumes, therefore, that brilliance is proportional to the logarithm of the stimulus intensity, a law which has exceptions at very high and very low intensities (*cf.* Fig. 38). It also assumes conditions of daylight or scotopic vision.

reversals of curvature at the spectral extremities. The function plotted in the figure assumes a spectrum of uniform energy, and conditions of daylight vision such that brilliance can be regarded as proportional to the logarithm of the stimulus intensity.

However, when experiments are made with different intensity levels it is found that the curve itself undergoes important variations, consisting in a displacement of the entire function along the wave-length scale, without essential change in form, the maximum lying at 554 millimicrons for high intensities but at 511 millimicrons for lower intensities. Since all portions of the curve are displaced proportionately, this change involves a reduction of the brilliance due to the longer wave-lengths, accompanied by an increase in that due to the shorter wave-lengths, as intensity is decreased. Concomitantly with this shift in the general position of the curve, with decreasing intensity, there is an arithmetically equivalent reduction of all of its ordinates. These latter changes need not concern us here, since they will be considered in our study of the determination of brilliance by stimulus intensity. (See page 76, below.)

252. **Visibility Curves.** — As noted above, in investigating the relation between brilliance and wave-length, recourse is usually had to indirect methods of measurement and representation. The most important of these are embodied in so-called *visibility or luminosity curves.* These curves are an attempt to isolate the essential functions which underlie the connection of brilliance and wave-length, eliminating changes due to intensity, etc. A visibility curve represents the capacities of unit intensities, at different wave-lengths, to evoke brilliance. More technically stated, such a curve is a plot of the reciprocal of the radiant intensity required, at various wave-lengths, to evoke equal brilliance. Such measures are valuable because, within certain limits, the form of a visibility curve turns out to be independent of the absolute value of the brilliance or stimulus intensity in question, making the problem a matter of relative intensities. The visibility method also has the practical advantage that it rests wholly upon the establishment of *equations of brilliance* and not upon the more precarious process of stepping off just noticeable differences.

Very careful studies have shown that, as partly implied by the facts already discussed above, there are two fundamental visibility functions, the one holding for all stimulus intensities above approximately 60 photons, and the other for all intensities below approximately 0.5 photons. Between these two intensity values, transition curves are effective, such curves apparently representing different ratios of participation of the two fundamental functions. The high intensity curve has its maximum at about 554 millimicrons and decreases to a value of 1% at 429 and 683 millimicrons on the two sides, respectively. Standard photopic visibility values are given in Table VI. The low intensity curve, as indicated, has its maximum at 511 millimicrons, decreasing to 1% values at approximately 400 and 610 millimicrons, on either side of the maximum. According to Hecht and Williams,[385] the two fundamental visibility curves are almost exactly similar in shape, when plotted on the same scale, the low intensity curve representing the high intensity one as shifted 43 millimicrons towards the shorter wave-lengths. Both curves exhibit a notable symmetry, although the high intensity one shows a relative depression of values on its short-wave slope.

TABLE VI

Average Normal Visibility Values

Adopted as Standard by the Illuminating Engineering Society and the Optical Society of America [386]

Wave-lengths	*Adopted Mean I. E. S.*	*Absolute Visibility*
400	0.0004	0.27
10	.0012	0.80
20	.0040	2.7
30	.0116	7.72
40	.023	15.3
450	0.038	25.3
60	.060	40.0
70	.091	60.7
80	.139	92.6
90	.208	139

TABLE VI — *Continued*

Wave-lengths	*Adopted Mean I. E. S.*	*Absolute Visibility*
500	0.323	216
10	.484	322
20	.670	446
30	.836	557
40	.942	629
550	0.993	662
60	.996	663
70	.952	641
80	.870	580
90	.757	502
600	0.631	421
10	.503	336
20	.380	253
30	.262	175
40	.170	113
650	0.103	68.8
60	.059	39.3
70	.030	20.0
80	.016	10.7
90	.0081	5.4
700	0.0041	2.7
10	.0021	1.4
20	.0010	0.67
30	.00052	0.35
40	.00025	0.17
750	0.00012	0.08
60	.00006	0.04
Wave-length of maximum	556	

253. **The Purkinje and Allied Phenomena.** — Vision which occurs under the dominance of the high intensity visibility curve is known as *photopic,* while that which is characterized by the low intensity curve is called *scotopic.* There are a number of interesting effects which rest upon the transition from photopic to scotopic vision, or *vice versa.* The one which is most frequently discussed is the so-called

Purkinje phenomenon. It consists in a reversal of the brilliance contrast between a red and a blue, in consequence of a reduction in the general level of illumination, when the red is somewhat brighter than the blue at the higher level. This change is obviously explicable in terms of the decrease in the relative visibility of the long, as compared with the short, wave sections of the spectrum, accompanying the replacement of photopic by scotopic response.[387]

For the majority of observers, the Purkinje phenomenon is entirely absent when the color pattern is confined to the center of the visual field and has an angular size not exceeding three degrees.[388] This corresponds with the fact that this region is normally devoid of scotopic sensibility, having a high threshold for brilliance, and consequent "night-blindness." An effect similar to that of Purkinje, and having an identical explanation, results when a red-blue pattern is shifted from the center of vision towards the periphery, under conditions of twilight vision. In order to obtain these effects satisfactorily it is necessary that sufficient time be allowed under the low intensity illumination to yield a considerable degree of dark adaptation. (See page 96, below.)

Other phenomenal changes, resting upon the transition from photopic to scotopic response, will be discussed in connection with the facts of flicker, acuity, etc. We may note, incidentally, that, at intensity levels which yield complete scotopic vision, there are no *chromatic* representations of the wave-length characteristics of the stimulus. The meaning of this will be considered in greater detail at a later point in our discussion.

254. **Light as a Psychophysical Concept.** — Illuminating engineers have chosen to define light in terms of the photopic visibility function, because the latter characterizes conditions of daylight vision. Intensities at which the scotopic curve becomes dominant are so low as to render efficient visual discrimination impossible. However, in spite of these facts, the definition of light must be regarded as being largely arbitrary and as dictated by practical pur-

poses. As we have seen, there are various measures of light, such as the lumen, candle-power, illumination and brightness. The first may be regarded as the most fundamental one, although candle-power is historically prior to it. The flow of light from a source, measured in *lumens,* is defined as being equal to the flow of radiant energy, multiplied by the absolute visibility of the particular kind of energy which is involved. In general, light is treated exactly as if it were radiant energy, except that it is evaluated, as to quantity, in accordance with visibility concepts.

Measures of absolute visibility can be expressed in terms of lumens and any convenient unit of *power,* the watt being the one which is most frequently employed. In general, if W is the radiometric value, V the absolute visibility, and L the light or photometric value, we have

$$(1) \qquad L = V W$$

According to Nutting,[389] the visibility function can be represented by the equation,

$$(2) \qquad V = V_m R^a e^{a(1-R)}$$

where $R = \lambda_{max}/\lambda$, λ_{max} being the wave-length for the maximum point of the curve and λ the wave-length for which the visibility is being calculated. $a = 181$, V_m is the absolute visibility at the maximum, and e is the base of the natural system of logarithms. Substituting in equation (1), we have

$$(3) \qquad L = V_m R^a e^{a(1-R)} W.$$

Now, when $\lambda = \lambda_{max}$, we have

$$(4) \qquad L = V_m W,$$

from which,

$$(5) \qquad V_m = L/W$$

for this particular wave-length, approximately 556. Consequently, V_m must measure the number of lumens per watt at the wave-length in question. This is the reciprocal of the so-called "mechanical equivalent of light." Its value is approximately 617.[390] The magnitude of the expression, $R^a e^{a(1-R)}$ should be equal, for each wave-length, to the coefficient of visibility which is plotted in Fig. 37. Knowing V_m and the visibility coefficient, we can determine the

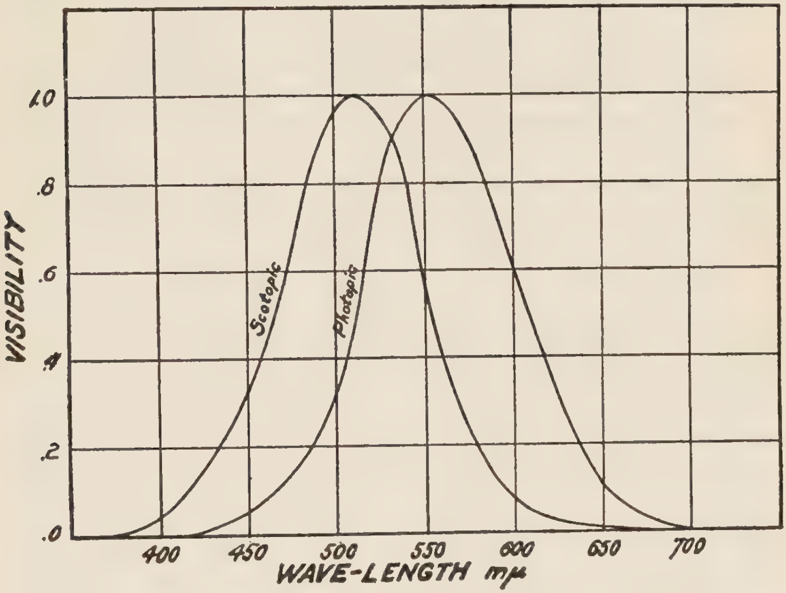


Fig. 37. The Scotopic and Photopic Visibility Curves of Human Vision.

These curves are based upon the work of Hecht. They show the scotopic and photopic functions to be extremely similar in form, the former having its maximum at about 511 mμ, while the latter is maximal at approximately 554 mμ. (Hecht places the photopic maximum at this wave-length, rather than at 556 mμ, as in the Optical Society data.)

lumens per watt for any wave-length, or for any mixture of wave-lengths.

It is evident that light, as thus conceived, is neither a physical nor a psychical quantity. It is, rather, a psychophysical notion, involving C. G. S. units, on the one hand, and a psychical dimension, which we may designate as ψ, on the other. Light can neither be identified with brilliance nor with radiant energy. It has the properties of both, taken together. Insofar as physicists and engineers think in terms of this notion, they are basing their thought in a very definite way upon psychological principles.

It may be noted that the unit of light-emitting power, the candle, is an arbitrary and naïvely chosen standard, involving a meaningless relationship between the physical and the psychological factors which are involved. When visibility is expressed, *absolutely,* in terms of lumens per watt, the values are significant only of the original arbitrary choice of the candle as a standard. It would seem more reasonable, now that we understand the principles which are involved, to define the unit of light upon a more rational basis. This could be done by setting the mechanical equivalent of light equal to unity, so that, at the maximum of the visibility curve, measures of light and of radiant power would be equal. The unit of luminous flux would then have about 1/617th of its present intensity.

255. Methods of Heterochromatic Photometry. — In establishing equations of brilliance between luminous stimuli of different wave-length compositions, difficulty is encountered on account of the accompanying chromatic differences. This gives rise to the problem of *heterochromatic photometry.* Brilliance comparisons are possible, even in the presence of extreme differences in hue or saturation, but the differential threshold for brilliance increases as a function of the concomitant chromatic dissimilarity. I have shown that, for chromatic differences within the spectrum, this function follows the equation of an ellipse.[391] However, the most satisfactory results are obtained by use of the so-called flicker photometer," [392] by means of which the two lights to be compared can be alternated in the same field, their relative values being adjusted so as to yield a minimum degree of flicker. They are then regarded as being photometrically equal.

II. Brilliance as a Function of Intensity

256. The "Absolute Threshold." — When the eyes are unacted upon by any external stimulus, the brilliance is ordinarily not equal to zero. This means that the accompanying color experience is a gray, rather than an ideal black. This gray is sometimes described as the "idio-retinal light," because it is supposed to involve a self-activity of the visual system. The most primitive question regarding the dependency of brilliance upon intensity is that of the absolute threshold, or the smallest quantity of light which will yield a characteristic visual experience. This evidently means the evocation of a brilliance which is just noticeably greater than the idio-retinal gray.

The intensity which is required at the absolute threshold, thus defined, is itself a function of a large number of conditions. If we specify the intensity in radiometric terms, the threshold must depend upon the wave-length, in accordance with a law resembling the reciprocal of either the photopic or the scotopic visibility curve. Which one of these applies must be determined by position in the visual field and, to some extent, by the state of adaptation. The photopic curve will be effective in a three-degree central area and the scotopic one will control the result in the periphery. However, if we express the intensity in light value, the influence of wave-length becomes less marked, disappearing entirely for the central field. If a three-degree central stimulus spot is employed, the absolute threshold is in the neighborhood of 0.05 photons. For a wave-length having maximum visibility, this corresponds to about 2.75 ergs per second per square meter. The peripheral threshold with full dark adaptation is approximately one ten-thousandth of this value.

When the area, or angular size, of the stimulus is progressively reduced, a point is finally reached at which the illumination required for the threshold begins to increase. It is found that, for small stimulus sizes, the liminal flux of light or energy is independent of size. Various investigators[393] agree that the absolute peripheral threshold for very small stimuli, such as stars, is of the order of magnitude of 10^{-9} ergs per second. At this rate, it would take forty years for the eye to absorb a single erg of energy; although the rate corresponds to about two hundred ultimate radiation quanta per second. Assuming that we can see the faintest star in a fifth of a second exposure, the total number of ergs required for vision would be about 2×10^{-10}. Some estimates place the minimal number of quanta in the neighborhood of ten. It appears that the sensitivity of the eye to radiant energy is about three hundred thousand times as great as that of the most sensitive radiometer.

257. Supraliminal Brilliance as a Function of Intensity. — The visual process not only exhibits extraordinary absolute sensitivity, but it is also capable of covering an extremely wide range of intensities. Thus, the peripheral threshold with complete dark adaptation corresponds to a stimulus surface brightness of about 0.000015 candles per square meter, while the brightness of the disk of the sun approaches 1,000,000,000 of the same units. White paper in direct sunlight may have a brightness of 100,000, while certain tungsten lamp filaments exceed 16,000,000 candles per square meter. Some of these extreme brightnesses are, of course, physiologically injurious, the range of best vision lying between about 30 and 3000 of these units.

If we hold the wave-length composition of the stimulus constant, we can establish a definite relationship between its intensity and the resulting brilliance, measured in number of just noticeably different steps above the retinal gray. The function which is determined in this manner is shown graphically in Fig. 38, the intensity being plotted logarithmically. This method of plotting not only has the advantage of condensing the intensity scale, but of demonstrating that, over a rather wide range of medium intensities, the relation conforms to an equation of the type, $b = k \log i + a$, where a and k are constants, and b and i are the brilliance and the intensity, respectively. This is a formulation of Fechner's law for visual intensity response. The logarithmic relationship implies — as Weber's law — that the just

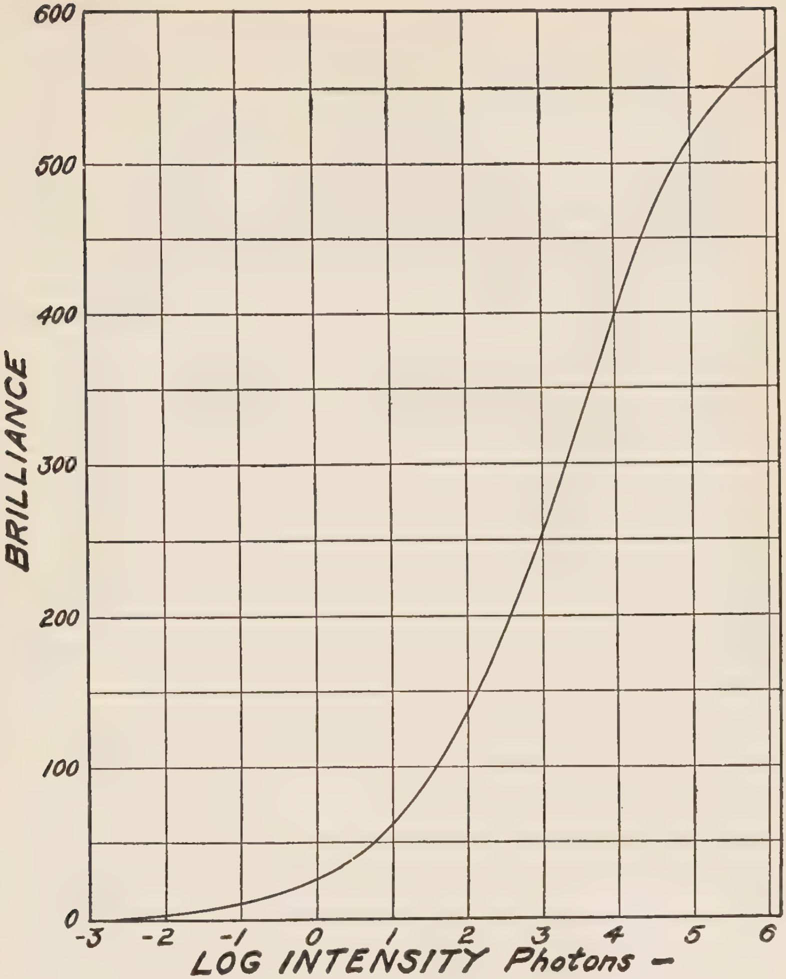


FIG. 38. BRILLIANCE AS A FUNCTION OF STIMULUS INTENSITY.

This curve was produced by graphical integration of the data represented in Fig. 39. Some distortion of the curve was necessary in the higher intensity region to make it conform to König's finding of a total of 572 steps, but this discrepancy is not serious.

noticeable fractional increment of intensity is a constant. Fig. 39 shows the actual dependency of the fractional increment upon intensity, as found by König and Brodhun, Aubert, and Blanchard. König and Brodhun found that the values of the threshold differ for different wave-lengths at low intensity but are independent of wave-length in the high intensity region. This is probably due to the fact that their data involve a mixture of photopic and scotopic vision at low intensities, but naturally not at high intensities. The law may be presumed to have a different form for the two types of visual response, and the ratio between the two would be a

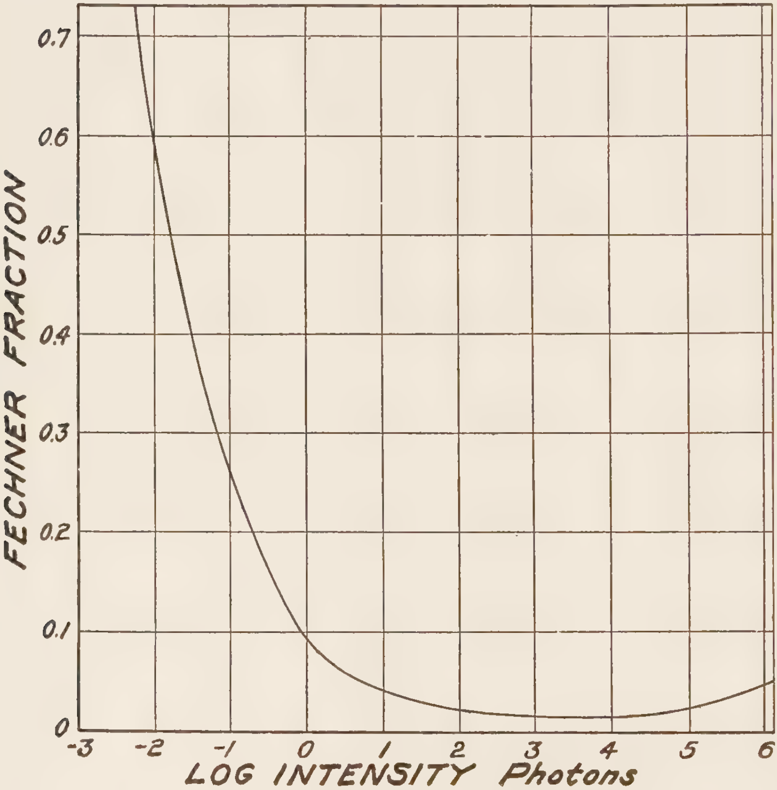


Fig. 39. The Relative Threshold as a Function of Stimulus Intensity for Vision.

This curve was replotted from Hecht's averages of the data of Aubert, Blanchard and König and Brodhun. Being in terms of photons, it is independent of pupillary size.

function of the wave-length at constant brightness. Nutting[394] has suggested the formula,

$$P = P_m + (1 - P_m)(F/F_0)^n \tag{6}$$

to represent the relationship between the relative threshold and the brightness level. P represents the threshold, P_m its minimal value, F_0 the brightness at the absolute threshold and F the given brightness.

The failure of the brilliance-intensity law to follow a strictly logarithmic equation is to be expected, since such an equation would demand that the brilliance should be equal to minus infinity at a zero value of intensity, and also that it should become plus infinity at infinite intensity. We can assign no empirical meaning to a negative brilliance, especially an infinitely negative one; and it is scarcely to be expected that the psychophysiological system of vision can keep pace with excessively high stimulus intensities. The manner of departure of the brilliance-intensity law from logarithmic form at low intensities corresponds to the effect of adding a constant intensity which is independent of the stimulus. The theoretically required intensity agrees in general magnitude with the brilliance of the idio-retinal light.

The exact value of the relative threshold varies rather widely with conditions, but is of the order of magnitude of 1/100th part, or 1%, for the intensity range within which the logarithmic relationship holds. Difference in chroma between the two areas which are being compared, the nature of the dividing boundary, the brilliance of the surrounding field and numerous other factors contribute to the determination of the threshold. Helmholtz[395] was able, under the best conditions, to appreciate a stimulus difference as small as 1/167, or 0.6%, while the results of König[396] show no values lower than 1.7%.

Schjelderup[397] regards Weber's law, in vision, as being merely a special case of a more general principle, expressed by the equation:

$$\Delta i = ai + bI, \tag{7}$$

where i is the intensity of the test-field stimulus, I that of the surrounding field, and a and b are constants. When i is greater than I, Weber's law holds approximately, but with the reverse condition, it breaks down seriously. With fields smaller than one degree, when I is greater than i, the differential threshold may become independent of the test-field intensity, but proportional to that of the surrounding field. These relationships are probably to be explained in terms of the scattering of light within the eye. The usual experimental condition for the study of brilliance discrimination laws involves a completely dark surrounding field. Cobb[398] and also Dittmers[399] find, however, that the differential threshold is at a minimum when the test and the surrounding fields are of the same brightness.

258. Brilliance and Wave-Length Composition. — When, as is ordinarily the case under any but laboratory conditions, the stimulus acting upon the retina is not of a single wave-length but consists of a mixture of wave-lengths having different intensities, the problem appears as to the manner in which brilliance depends upon the *composition* of the stimulus. The simplest statement of the general operative principle in this case, is that the photometric values for the different combined wave-lengths *add arithmetically*. This means that if we were to divide a complex stimulus into any desired number of individual components and then were to determine the photometric brightnesses of each of these components, the sum of the values thus obtained would be the photometric brightness of the original undivided stimulus. This principle is sometimes called the additive law for luminosities. It permits us to infer a more strictly formulated psychophysical relationship, as follows: The brilliance which is evoked by any simultaneous combination of radiant energies of different wave-lengths is equal to the Fechner function of the sum of the several radiant intensities, each multiplied by its own absolute visibility. The term, Fechner function, is used to designate the approximately logarithmic relationship of Fig. 38, above.

The validity of this so-called principle of the additive combination of luminosities has been the subject of considerable controversy and numerous experiments.[400] It seems that the answer may depend upon the method of photometry that is utilized in measuring the stimuli which are to be combined. However, the principle is generally conceded to hold within the intensity ranges of either exclusive photopic or exclusive scotoptic vision with photometry by "direct comparison." Departures are to be expected in the zone of overlap of these two systems, and it is necessary, in general, to make the measurements of the individual constituents under conditions which are exactly similar to those employed for their combination.

III. BRILLIANCE AS A FUNCTION OF SPATIAL FACTORS

Brilliance, considered simply as a component of visual experience, is determined in important ways by spatial and temporal aspects of the stimulus. In the present paragraphs, we shall neglect the pattern aspect of the experience, *per se,* and consider only how the brilliance values at particular points in the visual field may be controlled by processes at other points, or how they may vary as functions of mere position. These two types of dependency may be designated as *pattern functions* and *field functions,* respectively. The mode of determination of patterns and positions, as such, will be considered separately in later paragraphs.

259. **Field Functions.** — The brilliance which is evoked by a stimulus of fixed photometric intensity varies with position in the field of vision, being, in general, greater in the periphery than in the center. The difference between these two positions increases tremendously as the level of scotopic dark adaptation is raised. We are unable to specify the exact manner in which the brilliance values change as a function of position, because reported tests have been made for threshold brilliance, only. Such studies show that, with complete scotopic dark adaptation, the threshold is about ten thousand times higher for a small stimulus (say one

degree) in the center of the field than it is in the mid-periphery. The change occurs very rapidly as the stimulus moves out of the central position, being complete beyond about five degrees. Corresponding changes in degree of brilliance are to be expected when the stimulus is well above the threshold.

However, under conditions of photopic bright adaptation, it is likely that the center of the field will yield the superior brilliance. The exact manner in which brilliance varies with position in the visual field depends upon the wave-length, or wave-length composition of the stimulus. Under scotopic dark adaptation, a long-wave stimulus (a red) will show no brilliance increase in passing from center to periphery, since it is purely photopic in its effect.

260. Pattern Functions Involving Area. — We have already noted that the stimulus intensity, which is required to yield a just noticeable elevation of the brilliance above the idio-retinal gray, depends radically upon the angular size, when the latter is small. In the center of vision, when the angular diameter does not exceed about 50 minutes of arc, the threshold intensity is inversely proportional to the (angular) area. For larger sizes, this constancy law breaks down, but the intensity threshold does not become independent of size until a diameter of about four degrees is reached. In the periphery of the visual field, an exclusively photopic stimulus shows a reciprocal relation between area and intensity, for the threshold, up to a diameter of about half a degree. An exclusively scotopic stimulus, on the other hand, reveals a reciprocal relationship between intensity and stimulus *diameter* within the same size range.

Quantitative studies appear to be lacking with regard to the absolute brilliance values which attend supraliminal stimuli of considerable intensity and small area. Presumably, the brilliance is a function of the total radiant power affecting the eye, rather than of the intensity — power per unit area — alone. If stimuli of small area and low intensity are also of brief duration, there is a tendency for the triple product of these factors to be constant, so that the threshold, and probably any reasonable supraliminal brilliance, is a function of the total amount of *energy* received. This principle can be understood more completely when we come to consider the law of growth of brilliance in time. Piéron[401] has shown that, both in the center and in the periphery of the visual field, the very lowest energy threshold accompanies very brief durations (20 and 2 σ, respectively) and relatively large stimulus areas.

261. Pattern Functions: Contrast. — In the phenomena which we have just considered, the brilliance evoked on a given visual area is augmented as a result of similar excitation in an adjoining area. In the effect known as contrast, on the other hand, there is a reduction of brilliance, due to excitation in adjoining regions, or an enhancement due to the relative absence of such excitation. We may distinguish between two interacting areas of this sort by calling one the *test field* and the other the (contrast-) inducing field, the former being, in a typical instance, a single area, such as a circle, completely surrounded by the inducing field. In general, the contrast effect is a function of the difference in brilliance or in stimulus intensity (photometrically expressed) between the two fields, and may be taken as zero when the fields are indistinguishable. It is found that brilliance contrast depends upon stimulus intensities through the medium of the visibility curve so that, as in other cases considered above, photometric intensities form the most convenient stimulus measure in studying this effect. Brilliance contrast is, at least to the first order of approximation, independent of wave-length and hue, except insofar as brilliance itself is thus dependent.

Numerous authorities agree that the contrast alteration (increment or decrement) of the equivalent brightness of the test field is *proportional* to the brightness difference between the test and inducing fields. By " equivalent brightness " is meant the photometric stimulus intensity required to match the test field in brilliance in the absence of the given contrast influence. According to Hess and Pretori,[402] the equivalent brightness of a small test field surrounded by a relatively dark inducing field remains constant when the brightness increments of the two fields are proportional. Both of these laws are undoubtedly true only for a moderate range of values, breaking down under extreme conditions. When the relative areas of test and inducing field are varied, the contrast effect varies directly as the square root of the area of the inducing field and, within certain limits, inversely as the diameter of the test field. The contrast influence exerted between the two fields is actually mutual, although it is more evident in the case of the smaller when the two are of unequal area. The increment or decrement due to contrast is greater at the boundary between the fields than elsewhere, so that it is possible to distinguish between border contrast and surface contrast.

We have already noted that contrast, or an inducing field, influences not only absolute brilliance values, but also differences between such values, when the test field itself exhibits a brilliance pattern. According to Hess,[403] a very bright inducing field can render invisible an original brightness pattern having an intensity ratio of 1 : 800. As already noted (*cf.* page 79, above), a number of investigators have shown that the just noticeable difference in brilliance within the test field is a function of the brilliance of the surrounding field.

IV. FUNCTIONS WHICH DETERMINE BRILLIANCE PATTERNS

We may now consider a few principles which are involved in the control of brilliance patterns, within the subjective visual field. In the preceding paragraphs, we have dealt with the way in which brilliance values at fixed points depend upon pattern, and we have now to discuss relationships which are of the converse order.

The general laws which govern the relation between the spatial configuration of the visual stimulus and that of the corresponding picture on the subjective projection field can be inferred immediately from the principles which we have already laid down in our discussion of visual perception. If we regard the stimulus phase as beginning at the point where the rays impinge upon the cornea of the eye, we must say that the physical configuration of the extraocular stimulus consists almost exclusively in a pattern of *ray directions*. At each point on the cornea, rays are arriving from *all* points in the object field, so that the details of the latter have a practically complete representation at any such corneal point. If we trace any one of these directional patterns, rectilinearly, through an intersection point of this sort, and if we project the result upon a surface, such as the retina, we can reconstruct a projection of the objective field pattern. Ordinarily, this is done by extending the rays through the so-called *nodal points* of the eye, rather than through a point on the corneal surface. In our discussion of the refractive relationships of brilliance, below (see pages 97–115), we shall consider this matter in somewhat greater detail. The pattern relationships of the stimulus are more readily expressed in terms of the retinal image than in those of a conflux of rays at the cornea or pupil. Furthermore, the retinal configuration presents features which are of far greater interest.

262. Acuity as a Function of Stimulus Intensity.— In our sections on visual perception, we have already considered some of the objective conditions which govern visual acuity. However, we have postponed a treatment of its dependency upon stimulus intensity, because this can be stated most completely in terms which involve ocular conditions. Acuity depends, in part, upon the optical resolving power of the eye, which varies with the size of the pupil, and also upon the amount of light which actually passes through the pupil from each feature of the object surface. This amount must obviously be a function of the pupillary area, so that the law which relates acuity to intensity is best expressed in terms of photons or analogous units. The most satisfactory study of the relationship in question is still that of König[404] made about thirty years ago. He employed the natural pupil, but his results can be corrected by mean of Reeves' pupillary data (see page 111, below) to yield a relationship expressed in photons; and given in Fig.

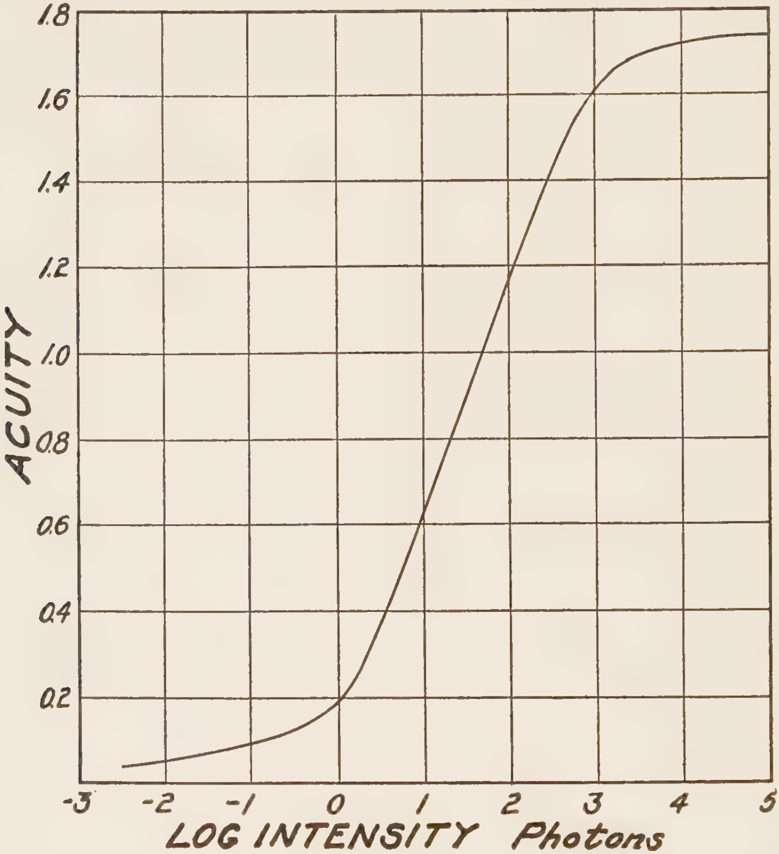


FIG. 40. VISUAL ACUITY AS A FUNCTION OF STIMULUS INTENSITY.

This curve was plotted from the data of König, as computed by Hecht for constant pupillary size, using Reeves' data with respect to the latter. However, it was necessary to multiply Hecht's results by a factor of 3.18 to correct for his definition of the "photon" in terms of millilamberts rather than candles per square meter.

40. It will be seen that this involves two logarithmic ranges, following equations of the general form:

$$a = b \log i + c, \qquad (8)$$

where a is the acuity, i the intensity and b and c are constants. The sudden change from one range to the other at approximately one photon corresponds to the shift from scotopic to photopic vision. The logarithmic law fails at about 500 photons and above about 2000 photons there is no further improvement in acuity.

The acuity, in these measurements, is taken as the reciprocal of the minimum separation between two lines, which will just permit of a double impression, the separation being formulated in degrees.

263. Irradiation. — Another set of relationships, which is more or less opposed to the acuity law, falls under the heading of *irradiation*.[405] A bright area, viewed in contrast with a dark background, increases in subjective size with augmented stimulus intensity. The linear increment is roughly proportional to the intensity, so that the effect is relatively more marked for small than for large areas. It is also greater when the accommodation, or focus, of the eye is imperfect. High intensities, well above those at which the acuity law ceases to be logarithmic, are required to yield marked irradiation phenomena. At such intensities, alternate light and dark lines of equal angular width on the stimulus side will be represented as unequal in the visual field, the brighter ones being the wider. Star images are also subject to similar effects.

We shall discuss the laws connecting patterns of retinal excitation with cortical and conscious configurations in subsequent Sections, dealing with "sensory projection." (See Volume III.) Although this topic can properly be considered from the sensory standpoint, we can treat it most economically under the heading of cerebration.

V. BRILLIANCE AS A FUNCTION OF TIME

We must now consider the relationships which hold between brilliance and the time after application or removal of the stimulus; or, in general, after any change in the three primary stimulus characteristics. It is a general principle with regard to these relationships that, after the lapse of a sufficient period, the characteristics of the visual consciousness become independent of the time, or reach an *equilibrium.* Consequently, the dependencies of vision upon time are restricted to relatively short intervals, although in certain cases these may be as long as an hour. We shall confine ourselves, in the ensuing discussion, to the effects produced by changing from a *zero* value of stimulus intensity to some finite value, or a reverse change. The effects which are produced by changes between two finite intensities follow laws which are generally similar to those in which zero values occur, although such effects have not as yet been studied in much detail. Where the modification of the stimulus is in wave-length or in wave-length composition, rather than in intensity, it will be possible, as a rule, to express the change, so that it has intensive significance, by employing photometric measures. The effects which are produced upon brilliance by such alterations appear to follow the same laws as those which result from alterations in stimulus energy.

264. The Time Threshold. — Experiments indicate that, when very brief stimuli are employed, the resulting brilliance depends upon the product of the stimulus duration and its intensity. In other words, the effect is dependent upon what is known to the physicist as *exposure.* There is apparently no exposure interval so small that it cannot evoke an appreciable brilliance, provided the accompanying intensity is sufficient to raise the product of time and intensity above that required by threshold exposure. The value of this latter threshold in terms of energy and seconds is dependent upon wave-length, in accordance with the visibility curve that is effective under the given conditions of experiment. If the intensity is measured in photometric terms, based upon the given visibility curve, the *exposure threshold* is constant for a given area and over a certain range of durations, increasing, however, for very small as well as for relatively large values of the time.[406] Above the threshold, the brilliance varies as the Fechner function (*cf.* page 76, above) of the exposure ($i \times t$).

265. The Growth Curve for Brilliance. — The above considerations indicate that, when the photometric intensity of a retinal stimulus is suddenly changed, the preëxisting brilliance value behaves as if it possessed inertia. The brilliance does not instantaneously assume the value which normally corresponds to the modified stimulus intensity, but rises or descends to this value during a finite period of time and according to a definite law. There is, in the first place, a very brief *latent period* during which no change at all occurs. If the stimulus intensity has been increased, the brilliance then begins to rise rapidly at first but with continuously diminishing speed, so as to approach a maximum asymptotically. For considerable intensity increments, the early portions of the curve are nearly straight and their steepness increases with increase in the photometric intensity of the stimulus, the initial rate of rise being greater the higher the intensity. The time required to reach the maximal brilliance value is called the *action time* of the stimulus, and according to Piéron[407] varies inversely as a power of the intensity, although other authorities find a logarithmic relationship. Recent measurements by Bills,[408] as well as the classical ones of Broca and Sulzer,[409] indicate that the action time, and hence the rate of rise, of stimuli having different wave-length compositions, are different even when their photometric values are the same, the brilliance values produced by the shorter wave-lengths in general rising more slowly than those produced by the longer waves. Other investigators find the curves to be dependent only upon photometric intensity. According to McDougall,[410] the action time of the minimal perceptible stimulus is one-fifth of a second.

266. The Decay Curve and Charpentier's Bands. — When the stimulus is cut off, either directly upon reaching its maximal effect or shortly thereafter, the brilliance at first decays rapidly and then more gradually, in accordance with a curve similar in form to that which governs its growth, but inverted. (See Fig. 41.) Under proper conditions of time and intensity, this decay is followed spontaneously by a rapid recurrence of a considerable brilliance value, which again decays, this process being repeated a number of times with diminishing maximal values of the brilliance. When the application of the stimulus and its withdrawal are accomplished by moving a band of light across the retina, these successive phases of brilliance rejuvenescence produce alternating light and dark bands which have been named for their discoverer, Charpentier.[411] Recent contentions, that the processes underlying these bands are either abnormal or artificial, are unconvincing.

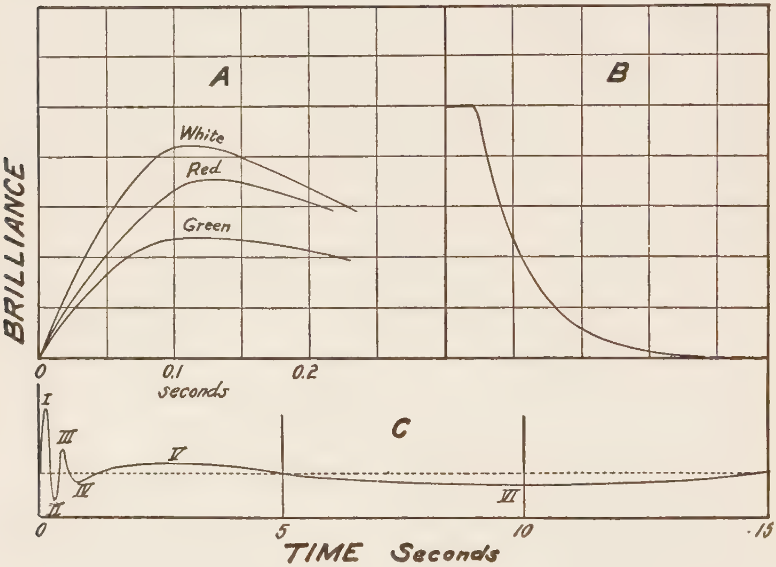


FIG. 41. BRILLIANCE AS A FUNCTION OF STIMULUS TIME CONDITIONS.

The curves in section *A* of the figure represent the manner of increase of brilliance as a function of time after the application of a steady stimulus. They are taken from the researches of Broca and Sulzer. Section *B* shows a schematic curve of decay following entire removal of the stimulus after the brilliance has become steady. Section *C* represents the oscillations of brilliance, to yield successive negative and positive after-images (as numbered) following the application of a stimulus of very brief duration. (This last diagram is due to C. Hess.)

267. Positive After-Images. — After the primary brilliance evoked by a brief stimulus has vanished, whether smoothly or intermittently, there may be a further recurrence of brilliance taking the form of so-called positive

after-images. Of these, at least three have been identified in addition to the primary image, each image being separated from its predecessor by a dark interval. In the case of a moving stimulus, the images spread out behind the primary impression like a series of comet-tails or satellites. The first after-image is named for its discoverer, Purkinje. Von Kries regards it as a phenomenon of scotopic vision which he conceives to be delayed with respect to photopic response, and this explanation was borne out by its seeming absence in the center of vision. More recently, however, Fröhlich [412] has shown that, with sufficiently intense stimuli, the image is obtainable centrally, but this may be due to the fact demonstrated by Abney that some observers have a slight amount of scotopic vision in the center of the visual field. Under proper conditions of intensity and adaptation, the Purkinje after-image is followed by a tertiary image, and this latter again by a quaternary one. Fröhlich believes, on the basis of careful studies of the laws which connect these positive after-images with intensity, area and time, that they represent phasic recurrences of excitation in central neurones.

268. Brilliance Flicker and Fusion. — When stimuli, having different intensity values, are rapidly alternated, the phenomenon known as *flicker* appears. This consists in a rapid pulsation of the brilliance. The violence of such pulsation increases with increasing intensity difference between the alternating stimuli, and also with decrease in their frequency of interchange. For each pair of stimuli, there is a frequency at which flicker disappears, the brilliance assuming a steady value as if the stimulus were constant. It has been shown that this so-called *critical flicker frequency,* or the number of alternations per second just sufficient to produce fusion, is proportional to the logarithm of the intensity of the stimulus when this is alternated with a dark, or zero intensity, phase. At high intensities, the law appears to be substantially independent of wave-length, or wave-length composition, provided the intensity is expressed in photometric terms; in fact, measurement of the critical flicker frequency has been employed as a method of photometry. At lower intensities, according to Ives, the proportionality constants depend upon wave-length, the slopes increasing in the order corresponding to blue, green and red, respectively, as shown in Fig. 42. At very low intensities, as shown also in the figure, there is a radical decrease in the slope for all wave-lengths, this change occurring where scotopic vision replaces photopic.

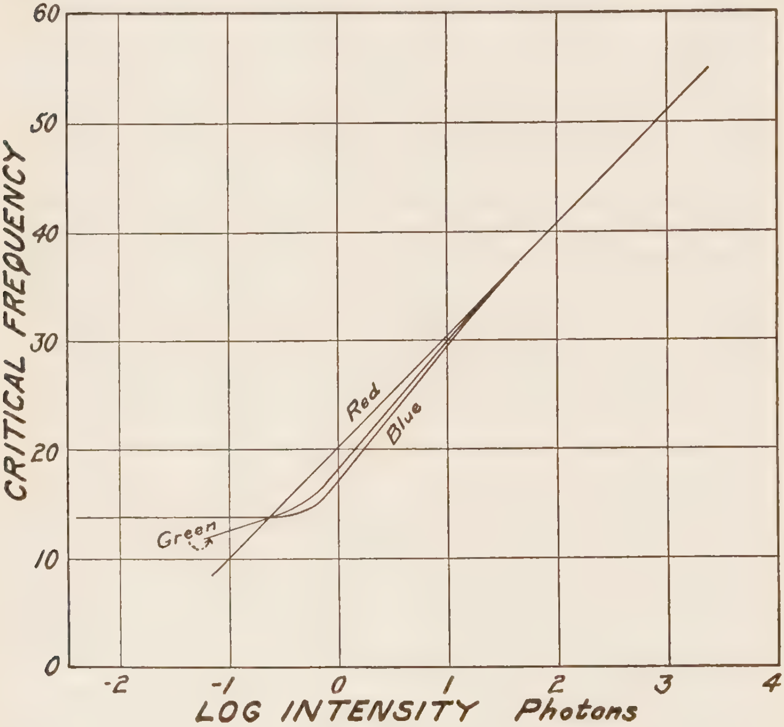


Fig. 42. Critical Flicker Frequency as a Function of Stimulus Intensity.

These curves show how the minimal rate of alternation of a stimulus of the indicated intensity with an equal interval of zero intensity, to just eliminate flicker, varies as a function of the intensity. The curves were reconstructed from graphs given by H. E. Ives.

The *Talbot-Plateau law* states that the brilliance resulting from the fusion of rapidly alternating stimuli, having different intensities, is identical with that which would accompany the same average flow of energy in continuous form. In other words, the fusion brilliance represents the time integral of the photometric intensity, divided by the time. This law has been very carefully tested and is accurately valid, except in connection with extremely high or extremely low intensities, or when fusion is not complete.

269. Photopic Brilliance Adaptation. — When the stimulus is permitted to act continuously upon the retina, over a considerable period of time, positive after-image and flicker phenomena are of course absent, but these are replaced by effects which lie at the basis of the so-called *negative after-image.* With a persistent constant stimulus, the growth of brilliance to its maximum is followed by a relatively gradual decline which goes on, with increasing rapidity, until an equilibrium condition is reached. The initial rate of decline is higher the greater the photometric intensity, being practically independent of wave-length and composition, but the time required to reach equilibrium is constant over a wide intensity range. The equilibrium time, however, is greater for large than for small areas, and varies with the location of the area in the visual field. Theoretically, the equilibrium condition is approached asymptotically but, practically, for photopic vision the time lies between one and two minutes.

It can readily be shown that the decline in brilliance, accompanying continued stimulation, rests upon a reduction of the *brilliance sensitivity* of the visual system. This condition persists after the removal of the original stimulus and has equivalent values for all stimuli. If we represent the brilliance sensitivity of the visual apparatus by unity, when it is in equilibrium with complete darkness, we can express the sensitivity, resulting from adaptation to any finite stimulus, by a fraction. Such fractional sensitivity can be measured by establishing an equation of brilliance, between the affected and an unaffected area, using different stimulus intensities. The sensitivities of two differently affected areas will then be inversely as the stimulus intensities which are required to produce the brilliance match. It has been shown by Von Kries [413] that, for a constant state of adaptation, such sensitivity values determine the condition for a brilliance match, acting as constant coefficients of the stimulus intensities regardless of the values assigned to the latter. This principle is known as the *Fechner-Helmholtz* or the *coefficient law.* As we shall see, this law, together with the concept of sensitivity, is valid not only for brilliance but also for the chromatic aspects of color. Abney [414] claims that the depression of brilliance sensitivity by a stimulus of one wave-length will show different values when tested by stimuli of other wave-lengths. Thus, exposure to a long-wave stimulus is supposed to depress red brilliance more than it does green or blue brilliance. Dr. Langford [415] and I have made numerous attempts to verify this alleged wave-length specificity of changes in brilliance sensitivity, and have been able to find only the slightest trace of it.

The tendency of the sensitivity to find an equilibrium will cause it to increase when the stimulus is removed, or when the latter is given a value below that for which equilibrium has been established. Such changes demonstrate a law which connects equilibrium sensitivity with stimulus intensity, expressed photometrically, according to which the former varies approximately in inverse proportion to the latter, maximum sensitivity being regained only under conditions of equilibrium adaptation to complete darkness.[416] The process of sensitivity reduction, under the influence of a stimulus, has commonly been called *retinal fatigue,* while the reverse change has been known as *retinal recovery.* On account of the possibly erroneous implication of these terms it would seem advisable to replace them by the terms, *minuthesis* and *auxesis,* which refer to the decrease or increase, respectively, of any specific sensitivity, without regard to any theory as to the mechanism underlying such changes.

It was Hering's belief that equilibrium adaptation involves the elimination of all brilliance differences, regardless of the stimulus pattern, and this would be logically necessary if the equilibrium sensitivity were exactly in inverse proportion to the stimulus intensity. However, I have shown[417] by careful measurements that reduction to a constant dead level of brilliance does not in fact occur, for all stimuli. The inverse relationship between intensity and sensitivity involves a power of the former somewhat smaller than unity, so that although adaptation tends to reduce the apparent differences between stimuli of diverse intensities, it does not completely eliminate them.

Negative After-Images.—Local differences between sensitivity values in the visual field are responsible for the phenomena known as *negative after-images.* Such images are best observed, after adaptation to a particular brightness pattern, if one looks at a uniformly illuminated surface. The areas which have been adapted to the brighter portions of the pattern then appear dark, while those which have been adapted to the darker portions appear relatively bright. However, it is easily possible to observe these negative images in the absence of any "reacting stimulus," on account of the local reductions produced in the idio-retinal light. Such observations indicate that the self-activity depends upon the sensitivity, and hence upon the same mechanisms which underlie excitation by external forces. Under appropriate conditions of successive exposure, positive and negative after-images alternate with one another in interesting ways. In general, we must suppose that adaptation begins immediately upon the application of the stimulus, so that all positive after-effects represent the net difference between a positive excitation process and an underlying reduced sensitivity.[418] For this reason the positive effects are most readily seen after brief exposures, when the sensitivity reduction is small.

Achromatic Dimming Effects.—I have shown[419] that after a negative after-image has been allowed to fade against a reacting field, it can be rejuvenated by a sudden *dimming* of the latter. Against the dimmed field, it again disappears, but if the field is brightened and then is dimmed once more, the after-image will again be visible. This process can be repeated over a period sometimes as great as twenty times that of the original life of the after-image on the undimmed field. If the reacting field is brightened instead of being dimmed, or *when* it is brightened after having been dimmed, a reversed or positive after-image can frequently be seen. These effects seem to be of a transitional type, indicating that the more bright-adapted areas follow changes in stimulus intensity more rapidly than do the less bright-adapted areas. This difference in inertia persists much longer than does the difference in static sensitivity.

270. Scotopic Adaptation. — Photopic adaptation, occurring at relatively high intensities or in a restricted central region of the visual field, follows laws that differ quantitatively from those of scotopic adaptation, which are associated with lower intensities and peripheral vision.[420] When a condition of daylight exposure is replaced by complete darkness, the brilliance sensitivity of the peripheral field increases, at first slowly, then more rapidly, and finally more and more slowly again. As in the case of photopic adaptation, the sensitivity approaches a limit which is practically reached after about an hour has elapsed, although by far the greater part of the change occurs during the first twenty minutes. Scotopic adaptation makes up for its slowness, as compared with the corresponding photopic change, by its vastly greater degree. Ordinarily, the latter brings about a sensitivity increase of about one hundred times, but the former in the normal subject may amount to a ten-thousandfold augmentation. The exact degree of scotopic adaptation depends upon the individual, some, who are said to be afflicted with "night-blindness," showing practically no scotopic increase. Scotopic adaptation carries the sensitivity of the peripheral visual field far above the highest sensitivity which is attainable in the center, so that in a state of complete dark adaptation the center of vision is relatively blind.

The scotopic, like the photopic, process arrives at an equilibrium with respect to any fixed intensity of stimulation.

When in a condition of dark adaptation, the intensity is suddenly raised, we have the unpleasant experience of being dazzled. The excessively intense brilliance over the whole visual field soon passes off, however, indicating that the establishment of equilibrium with respect to a high intensity occurs much more rapily than to a very low one. Negative after-images can be produced as a result of local scotopic adaptation, although such effects have been studied principally in connection with the photopic process. Positive after-effects are particularly brilliant with full scotopic dark adaptation and brief exposures.

Section 55

MONOCULAR REFRACTIVE RELATIONS OF BRILLIANCE

In order that the radiant energy which is reflected from, or transmitted through, an object of vision should become an effective visual stimulus, it must be focussed upon the retinas. The production of the retinal image depends upon the complex refractive processes which the radiant energy undergoes in passing through the media of the eye, these processes constituting the " sense-organ stage " of the visual response. A knowledge of the laws which govern the transit of the rays through the ocular media should permit us to deduce the properties of the retinal image from those of the radiation which impinges upon the eye. Such a knowledge involves the details of the structure of the eye as well as of its function. Structure may be in terms of gross anatomy, histology or chemical constitution, all three of these factors being included in visual physiology.

271. The Gross Anatomy of the Eyeball.[421] — The eye is essentially a camera, with a lens or refracting device in front and a sensitive film at the back to catch the image thrown by the lens. The film, in the case of the eye, is the retina. As shown in Fig. 43, the eyeball, or camera box, is roughly spherical in form and embraces three main coats. The outermost of these, constituting the mechanical casing of the eye, is known as the *sclerotic coat.* The main portion of the sclerotic is opaque, or at least translucent, and a portion of it appears as the so-called "white of the eye," but, in front, it becomes very transparent and bulges forward to form the *cornea,* through which the rays enter the eyeball and at the surface of which most of the refraction occurs. Within, and concentric with, the sclerotic is found the *choroid coat,* which is a vascular layer carrying the main blood vessels for the nutrition of the retina. Just as the sclerotic is continuous with the cornea, so the choroid merges into the tissues of the iris. Within the choroid coat, again, we find the *retina,* or nervous and sensitive layer of the eye. The retina ends abruptly in front with a jagged boundary known as the *ora serrata.* We shall consider the detailed structure of the retina below.

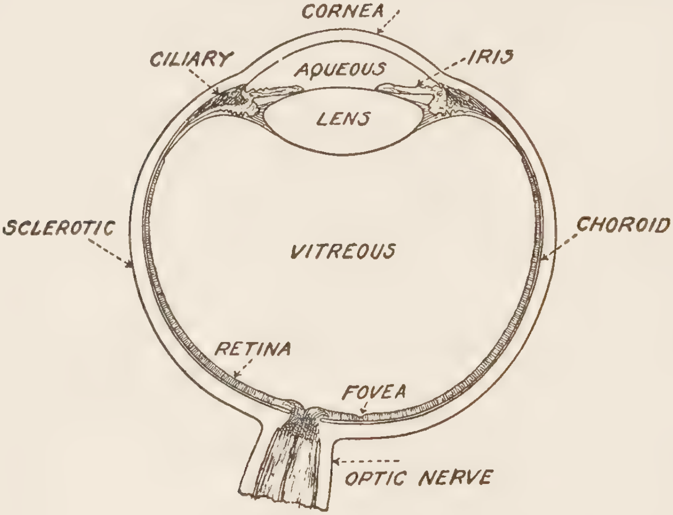


FIG. 43. CROSS-SECTION OF THE HUMAN EYE.

This figure represents a cross-section of the right eye, as viewed from above. Unimportant details are eliminated for the sake of clearness.

The Dioptric Parts. — The power of a lens to bend rays is commonly measured by means of a unit called the dioptry, which represents a refracting power bringing parallel rays to a focus at a distance of one meter from the lens. In terms of this unit, the refraction of the average eye is about 64, of which 43 dioptries belong to the front surface of the cornea. Behind the cornea we find a small chamber filled with a liquid called the *aqueous humor,* which is substantially identical with water. This humor bathes the iris and the front surface of the lens. The crystalline lens, as it is called, is a tablet-shaped body having a concentrically laminated structure, somewhat resembling that of an onion, its substance being of a high optical density which increases towards the center. The structure of the lens is such as to make it elastic, so that it can be made more or less oblate, according to the degree of tension applied to it by the suspensory ligament. This ligament surrounds the lens circularly and is continuous with the lens capsule or envelope. The tension on the ligament is controlled by the so-called ciliary muscles, which form a ring around the external rim of the ligament.

According to the theory first proposed by Helmholtz,[422] the resting condition of this mechanism, with the ciliary muscles uncontracted, corresponds to a state of maximal tension in the ligament and, hence, to the greatest possible flatness of the lens. In this condition, the refracting power of the latter is at a minimum and the normal eye is focussed on objects at an infinite distance. In the process called *accommodation,* which insures the production of sharp images of nearer objects upon the retina, the contraction of the ciliary muscles relieves the tension of the ligament, so that the inherent elasticity of the lens bulges the forward surface of the latter and thus increases its refracting power. In a ten-year-old child, the change in refraction, which is brought about in this way, amounts to 14 dioptries, but this amount decreases steadily with age, becoming zero at about eighty years, so that glasses with convex lenses are needed for near vision in old age.

The most common defects of focus in the eye are *myopia,* or near-sightedness, in which the image is formed in front of the retina and which requires a concave spectacle lens; *hypermetropia,* or far-sightedness, in which the image forms behind the retina and needs a convex spectacle lens; and *astigmatism,* which consists in a failure of horizontal and vertical lines to come to a focus simultaneously upon the retina, this last defect being corrected by means of a cylindrical lens. In general it appears that the eye is far from being perfect as an optical apparatus, although it is very wonderful as a product of evolution.

The Pupil. — The iris contains a variable circular aperture known as the *pupil,* the diameter of which ranges in the normal eye from two to eight millimeters, according to the intensity of the illumination. The average value is about four millimeters, the latter size being designated as the "physiological pupil." The motor mechanism of the iris comprises sphincter muscles for constriction and radial muscles for dilatation. The pupil which is seen in looking at another person's eye is a virtual image of the actual pupil, being considerably magnified; but nevertheless this image, or so-called *entrance pupil,* is the real determiner of the amount of radiant energy entering the eye. It is to be noted that a variation in the diameter of the pupil between two and eight millimeters corresponds to a change in area by a factor of 16, the accompanying alteration in the intensity of the retinal image being proportional to the pupillary area. It is customary to express the ability of a camera lens to illuminate the sensitive film or plate by means of a so-called "F number," which is equal to the diameter of the aperture, or pupil, divided by the focal length. Modern high speed anastigmat lenses of small focal length have F numbers as low as 1.9. For the eye with an eight millimeter pupil, the "speed" is F 2.85.

Behind the lens, and entirely filling the main chamber of the eye, is a gelatinous medium called the *vitreous humor.* This is highly transparent and has no important effect upon the formation of the retinal image.

The Optic Nerve. — At the rear of the eyeball, displaced to one side of the central line, is found the optic nerve, which receives the nerve fibres coming from all parts of the retina. At the point of attachment of the nerve, all of the layers of the eyeball are broken through, although the sclerotic coat is continuous with the envelope of the nerve. The perforation of the retina at this point is responsible for the so-called *blind spot* of the visual field.

272. The Minute Structure of the Retina. — Just as the eyeball as a whole is made up of a number of layers, so the retina itself is composed of a series of strata which, from within outwardly, are as follows: (See Fig. 44.) First, we find the layer of nerve fibres, running generally parallel to the wall of the eye and radiating from the exit-point of the optic nerve. Intermingling with these nerve fibres, are a few blood vessels. The next layer consists of so-called *ganglion cells,* which are the cell bodies belonging to the nerve fibres just mentioned. External to the ganglion cell layer is a stratum of so-called *bipolar cells,* which consist of short fibres bearing a cell body approximately midway of their length. These connect at one end with the ganglion cells and at the other end with the next following layer, which consists of the rod and cone cells. The latter constitute the actually sensitive portion of the retina.

Each rod or cone consists of three segments, and it appears that only the most external or so-called terminal segment is directly responsive to radiant energy. Outside of the layer of rod and cone cells, there is still a further stratum known as the *pigmentary epithelium,* consisting of hexagonal cells containing a black pigment, which apparently functions as a non-halation backing for the retina. In the frog's eye, under the action of strong illumination, the pigment granules migrate inwardly to surround the rods, but there is no evidence for this process in the human case.

The Structure of the Rod and Cone Cells. — Although possessing marked general similarities of structure, the rod and cone cells show unmistakable differences. As shown in Fig. 45, the internal segment of the *rod cells* consists of a fine thread, ending in a single knob and bearing a nucleus approximately in its middle. The mid-segment is quite elongate, has a granular material at one end and a longitudinally striated highly refractive composition at the other end, adjacent to the terminal segment. The latter appears to consist of a pile of small disks which are about five hundred

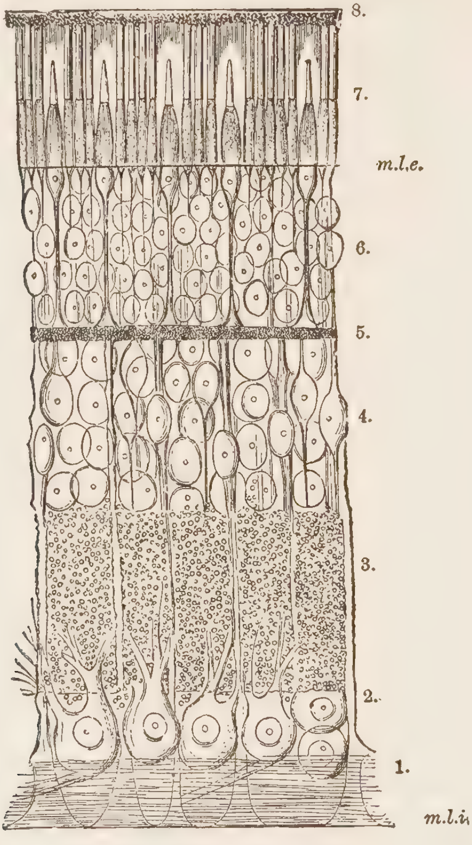


FIG. 44. A DIAGRAMMATIC SECTION OF THE HUMAN RETINA.

This drawing, due to Schultze, shows the histological structure of the retina in a parafoveal position, where both rods and cones are present. The various strata are as follows: (1) nerve fibres, (2) ganglion cells from which these fibres, as a class, emanate, (3) layer of synaptic junctions between ganglion and bipolar cells, (4) bipolar cell bodies, (5) layer of synaptic junctions between bipolar cells and receptor cells, (6) receptor cell nuclei, (7) receptors or rods and cones, and (8) layer of hexagonal pigment cells.

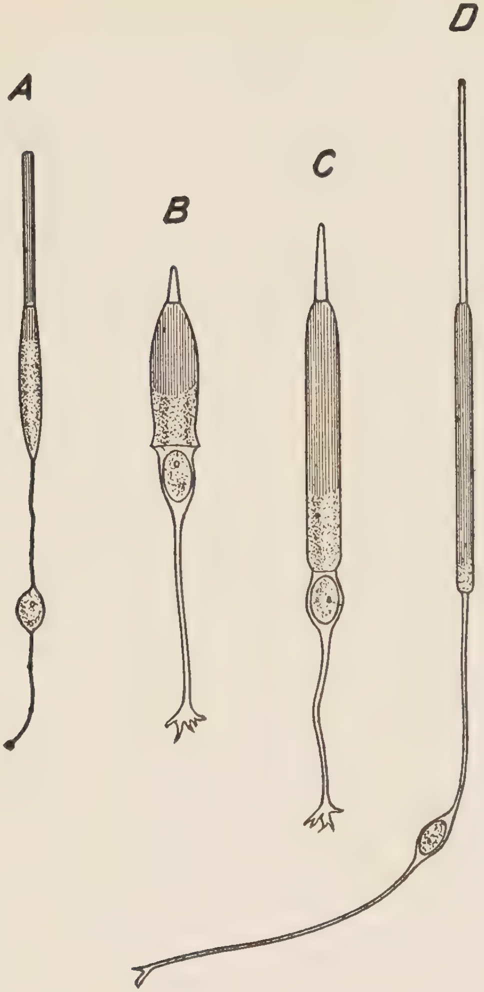


FIG. 45. RETINAL ROD AND CONE CELLS.

This figure shows typical retinal receptors in somewhat diagrammatic form. *A* represents a rod cell. *B* is a cone cell from the equatorial region of the eyeball, *C* a cone cell from near the margin of the fovea, while *D* is a cone cell from the central part of the fovea. These sketches are based on drawings by Greef as reproduced in *Quain's Anatomy*.

millimicrons in thickness and are so combined as to form a rod or cylinder.

The internal segment of the *cone cell* is much thicker than that of the rod cell and ends in a set of aborizations instead of in a simple knob; the cell nucleus is located close to the mid-segment, which is typically shorter and thicker than in the rod cell, although it contains similar differentiations of substance. The terminal segment of the cone cell, as the name implies, usually forms a cone-shaped protuberance instead of a rod. The rods are about 2000 millimicrons in diameter, while the cones range in diameter at their bases from 2500 to 7500 millimicrons.

If, as experimental data indicate, the terminal segments of the rods and cones are the primary visual receptors, it is evident that the radiant energy must pass through all of the more internal layers of the retina before it becomes effective. Consequently, the nerve impulse which is set up in the rod and cone cells must retrace the path of the radiant energy until it reaches the nerve fibre layer, after which it passes over the inner surface of the retina toward the optic nerve exit. It is clear that this so-called "inverted" structure of the retina demands that the inner layers should possess great transparency.

Local Differences in Retinal Structure. — Our discussion has already shown that there are local peculiarities of structure in the retina. For example, at the exit of the optic nerve, nerve fibres only are present and these run, not parallel to the eye coats, but through the latter.

One of the most important local peculiarities of the retina is to be found in the so-called *fovea centralis* which, as its name indicates, consists of a small depression at the intersection of the horizontal axis of the eye with the retina. The depression is due to the fact that at this point all of the retinal layers, with the exception of the cone cells, are swept to one side, exposing these cells to a maximally direct action of the rays. Here, as well as over a considerably larger concentric area, the rod cells are entirely absent, but the cones are packed so closely together and are so elongated that they appear to be rod-shaped. Measured in terms of the angle subtended at the nodal point of the eye, the diameter of the fovea is about one degree, while that of the rod-free region is approximately three degrees. The function of the fovea is evidently to subserve the greatest possible distinctness of vision, the clearing away of obstructions and the close packing of the receptors being obviously favorable to this end. Surrounding and including the fovea, is the so-called *macula lutea* or yellow spot, having a diameter of about seven degrees and containing a yellow pigment which absorbs the dangerous violet and ultraviolet rays.

According to Krause, there are about one hundred and thirty million rods in the retina, although Salzer places the number at half this value.[423] The total number of cones is estimated by Krause at seven million. From the center towards the periphery, the proportion of rods to cones increases continuously, there being three times as many rods as cones at the vertical equator of the eye. However, there is no place in the retina at which cones are entirely absent, cone vision still existing in the extreme periphery, although rod vision is quite absent in the normal individual in the extreme center.

273. Some Fundamental Conceptions in the Optics of the Eye. — Some very elementary notions, which are involved in any endeavor to deduce the characteristics of the retinal image from those of the eye and the external object field, may be mentioned. (See Fig. 46.) One of these is the conception of the *nodal point,* which is located within the crystalline lens where straight lines drawn from object points to corresponding retinal image points intersect. Although the rays entering the eye do not all pass through this point, the relations of object and image are substantially the same as if this were the case, or as if the lens system were replaced by a pinhole located at the nodal point. Lines drawn through the nodal point, from object to image, are called direction lines. The direction line which passes through the center of the fovea centralis is called the line of regard (*cf.* page 340, Volume I), and objects in the environment which this imaginary line intersects are said to be "fixated."

Given the object, such direction lines permit us to construct the image. Angles between these lines are called *visual angles* and indicate the angular size of the corresponding portion of retinal image. Visual angles, as they are effective at the retina, can be calculated directly from the size of the object and its distance from the eyes, since the angle outside of the eye is equal to that inside. It is better to specify visual sizes in angles than in units of length, even when the latter refer to the actual size of the retinal image. The linear size of an object evidently has a significance for vision which varies with the distance of the object from the eye.

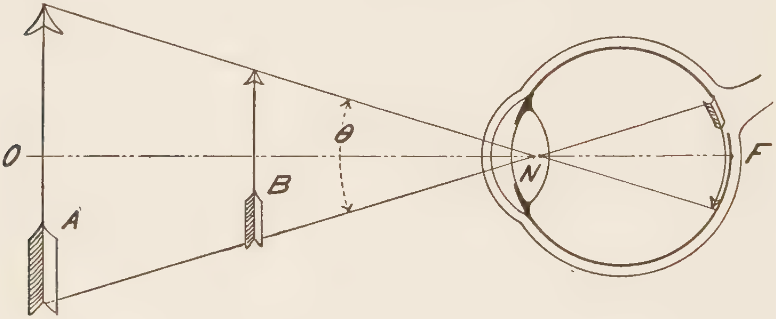


FIG. 46. DIAGRAM TO SHOW THE OPTICAL ACTION OF THE EYE.

At *N* are represented the two nodal points of the eye, while *F* represents the fovea and *O* is the point of fixation. θ is the visual angle subtended by either of the two arrows, *A* or *B*. It will be seen that, although these are at different distances, the sizes of their images upon the retina must be the same.

274. Further Intraocular Effects. — Although the study of direction lines establishes the main relationships between the visual object and the retinal image, there are numerous minor effects, resulting from peculiarities of the eye, which cannot be deduced directly from these relationships. One species of such effects is ascribable to various *aberrations* of the optical system, including the spherical, the chromatic and the astigmatic types. The first depends upon a failure of all rays from any single point in the object field to come to the same focus upon the retina, owing to variations in the degree of convergence from different zones of the pupil. The second form of aberration involves a similar discrepancy of focus in consequence of differences in wave-length, while astigmatism stands for focal differences between *lines* which make various angles with the plane of regard. Moreover, objects at different distances cannot, in general, be focussed simultaneously upon the retina, so that, ordinarily, some points in the object field will be definitely "out of focus." All of these effects tend to substitute a retinal area, or "diffusion circle," for a point, in the system of correspondence with object points.

Another class of intraocular effects is referable to small irregularities in the ocular media, causing an absorption, scattering or diffraction of the rays. Among these may be included the retinal blood vessels and the radially laminated texture of the crystalline lens. The former cast shadows, having a definite configuration, upon the receptor layer, while the latter are responsible for the "rays" seen on stars and other small points of light against a dark background. A further minor factor consists in the selective absorption of the light as it passes through the media of the eye. This brings about a modification of the distribution curve of intensity with respect to wave-length.

275. Entoptic Factors in Sensory Relationships. — It is evident that the whole group of psychophysiological relationships which we have considered in the preceding Section, for the case of the visual stimulus, can be restated for any phase of the optical intraocular process. We may consider that the domain of the stimulus extends from the corneal surface to the receptor layer of the retina, and that, at each point in this path, it is subject to some modification. Consequently, the psychophysiological relationships differ, at least slightly, for each position along the optic path within the eye. However, space does not permit us to examine the psychophysiology of all of these phases individually, and we must confine ourselves to the last step, namely, the effective *retinal image*. The latter consists in the mosaic of radiant energies which interpenetrates the rod and cone segments of the retinal receptors. On account of the general hemispherical structure of the retina, the image can be regarded as a segment of a spherical shell, having a very small thickness.

The image is somewhat roughened in texture by the optical irregularities of retinal topography, but it represents approximately, in point to point fashion, those superficies of external objects which are turned towards the eye. The representation is, of course, inverted with respect to the object field. Strictly speaking, we must consider the image, in its rôle as a stimulus, as being confined to the places where receptors are actually present. The receptors are packed closely together only in the vicinity of the fovea, being quite sparsely distributed towards the periphery, and being entirely absent at the place of exit of the optic nerve. Accordingly, the effective image has the structure of an irregular screen-plate reproduction, so that certain portions of the object field fail of representation at any given instant. The distribution of intensities and of wave-length compositions over the image are determined, point for point, by those of the corresponding object, or ray-sheaf, elements. (*Cf.* page 326, Volume I.)

In attempting to determine the nature of the psychophysiological functions which apply between the retinal image and visual experience, we must start with those which have been ascertained for the extraocular stimulus. We must then combine these latter functions with the relationships previously established for the extraocular stimulus and the retinal image. The extraocular factors can then be cancelled out, leaving us with the desired information.

276. Brilliance-Wave-Length Functions. — The first application of this kind of reasoning may be made to the relationship between brilliance and wave-length, the most significant embodiment of this relationship being the visibility curve. If the ocular media were completely non-selective in their absorption, what may be called the *retinal visibility curve* would be identical in form with the curve for the whole eye. However, the aqueous material of the eye is somewhat more absorptive for long than for short waves, while the pigment of the yellow spot is strongly absorptive in the "blue" and "violet." Combining these two influences, we obtain a transmission curve for the eye as a whole, as shown in Fig. 47. When this is applied to the photopic visibility curve of Fig. 37, it practically removes the asymmetry of the latter, which depends upon a relative depression of the visibility values on the short-wave side. The corrected retinal visibility curve can be represented, with a high degree of accuracy, by the simple probability function:

$$v = e^{-0.0002705(\lambda - 554.9)^2} \tag{9}$$

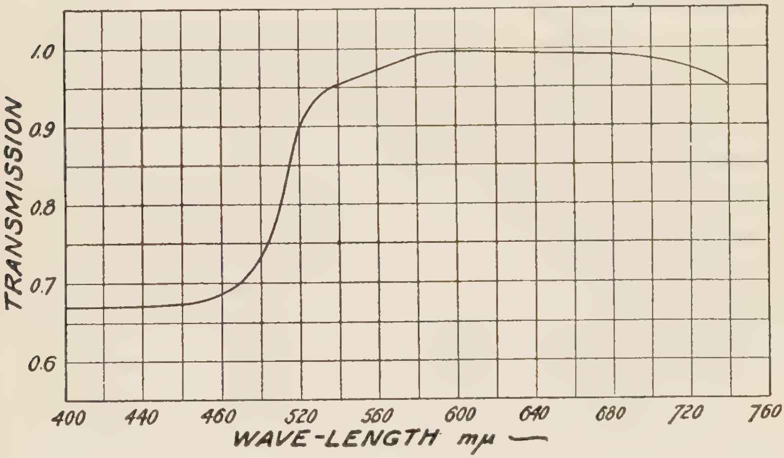


Fig. 47. Spectral Absorption Curve for the Ocular Media.

This curve shows how the transmission of radiant energy from the cornea to the retina varies as a function of wave-length. The strong absorption at the short-wave end is due to the macula lutea, or yellow spot, while the dip at the long-wave end is referable to the watery substance of the eye.

The fit of this function is much closer than is that between the uncorrected data and Nutting's asymmetrical function.

In addition to absorption changes, we may have to deal with a small amount of retinal fluorescence. This consists in a transformation of short waves into longer ones, the former usually being in the violet or ultra-violet regions. The radiant energy resulting from this transformation will ordinarily be of higher visibility than that which is trans-formed, so that the short-wave region should tend to have a falsely enhanced visibility value. This action is probably responsible for the departure of the corrected curve from complete symmetry, at the "violet" end, and for the frequently alleged visibility of ultra-violet rays.

277. **Brilliance-Intensity Relationships.** — *Retinal Illumination.* — The relationships between brilliance and intensity are dependent, in the first place, upon a formula which connects *retinal illumination* with the extraocular stimulus intensity. This formula may be written as follows:

$$i = 0.00416 \frac{ptd^2 \cos \phi}{(d - x)^2} I + A \tag{10}$$

where, i is the retinal illumination (or its radiometric analogue), I is the photometric brightness of the stimulus surface (or its radiometric analogue), in the direction of the eye, p is the area of the effective pupil, x the distance of the pupillary plane from the nodal plane of the eye, t the transmission of the whole eye for the type of radiation which is concerned, d the distance of the stimulus surface from the nodal plane, ϕ is the angle between the normal to the pupil and the line of sight, and A is a correction factor embracing the effects of scattering, fluorescence and the like.

By expressing our stimulus intensities in photons, we have already allowed for the influence of pupillary area, so that, under such conditions, p can be taken as equal to unity. For foveal stimulation, $\cos \phi = 1$, and the expression, $\frac{d}{d - x}$ departs from unity only slightly when d is large. Hence, for practical purposes, we can regard the retinal illumination as being proportional to the photon value, using a factor of $0.00416t$.

It must be recognized that, under ordinary conditions, the size of the pupil is a function of the retinal illumination[424] itself, following the curve given in Fig. 48. The natural action of the iris is in the direction of maintaining the retinal illumination constant. Of course, it cannot actually accomplish this result perfectly, on account of the small range of its effect, compared with the total intensity range of external stimuli. However, its ratio of 1 : 16 is obviously by no means negligible, and psychophysiological stimulus relations which have been established without the use of an artificial pupil,[425] or without due correction for the natural variations in pupillary size, must receive such correction before their retinal significance can be determined.

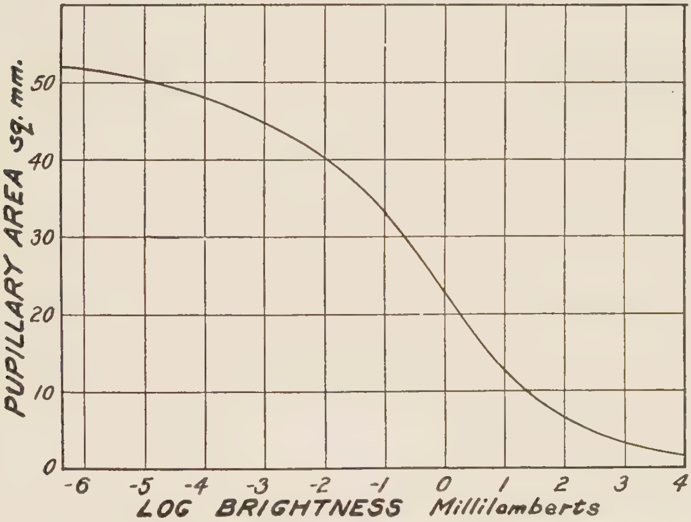


Fig. 48. The Dependency of Pupillary Size Upon Stimulus Intensity.

The curve shows how the area of the pupil changes with the brightness of the external stimulus surface, expressed in millilamberts. The data are those of Reeves, as plotted by Hecht.

Absolute Thresholds.—Using the formula which has been given above, we find that the absolute threshold for photopic vision corresponds to a retinal illumination of about .0002 meter-candles, that for scotopic vision being approximately .00000002 meter-candles. The energy values which have already been given, in our discussion of the extraocular stimulus, also apply equally well to the retinal image, since they are figured in terms of energy actually entering the pupil, and their precision is so low that the influence of ocular absorption can be neglected.

The Fechner Function. — The bearing of the intraocular factors upon the Fechner function requires relatively little attention, except for a change in the absolute intensity units which are used. The general form of the function remains unaltered, since it involves constant pupillary area and fixed wave-length composition. Variations in the character of the function, due to objective changes in the latter feature, may demand some correction in the curves, because of selective absorption by the ocular media. These changes will not be very important, owing to the very wide range of intensities which is involved. Similar considerations apply to the retinal version of the principle of the additive summation of luminosities.

278. **Effects of Scattered Light.** — It should be noted, however, that all of these relationships are subject to distortion, under special conditions, in consequence of the scattering of light in the eye. Thus, if we study the relationship between brilliance and intensity, with a surrounding field which is considerably more intense than is the test field, the retinal representation of the latter will receive a considerable amount of light which properly belongs to the surrounding area. Hence the fractional intensity difference which is presented in the test field will be less, retinally, than it is objectively. It follows that experiments, such as those of Schjelderup (*cf.* page 79, above), which involve the use of a bright surrounding field, may not be indicative of the true nature of the laws holding between the retinal stimulus and consciousness. This will be the case, particularly, when the test field is small and the surrounding field is large and relatively very bright. It is to be suspected that Schjelderup's principle of the proportionality of the relative threshold to the intensity of the surrounding field, under such conditions, may rest entirely upon entoptic scattering. This is also at least part of the basis of irradiation phenomena. However, it is certainly not possible to explain simultaneous contrast in general in this way (Fröhlich [426] to the contrary notwithstanding).

279. **Spatial Functions.** — The structure of the eye should be expected to have a considerable influence upon the

relations between brilliance and spatial factors. It should be clear, already, how the general pattern of the retinal image is determined by the refractive apparatus, on the basis of the directional properties of the rays which impinge upon the cornea. The distribution of brilliance over the subjective projection field correlates in a very definite way with that of radiant intensities over the retina. It is sometimes regarded as paradoxical that the visual picture in consciousness should be erect, whereas that upon the retina is inverted with respect to the object. However, as we have seen, the erectness of the conscious representation is primarily determined by subjective relationships which are independent of the objective orientation of the sense-organ. The axes of the visual field are fixed in definite ways with respect to the kinaesthetic vertical, the tactual field, etc., to form a closed system which is as nearly self-consistent as is possible. However, when once this system has been established, a departure of the retinal image from inversion must be followed by a proportional deviation of the subjective representation from erectness.

280. **Refractive Distortions.** — There are a number of characteristic distortions of form which can be attributed to optical defects of the eye, regarded as a refractive instrument. Perhaps the most prominent of these is the so-called "barrel distortion," which we have already discussed in our sections dealing with visual perception. (Volume I.) This is due to a failure of rays, falling upon the peripheral portion of the retina, to follow paths which are rectilinear through the nodal point of the eye. This type of distortion is to be found in many manufactured lenses. The various forms of aberration which we have discussed above also contribute to misrepresentations of objective forms under special conditions. Thus, chromatic aberration may be responsible for the appearance of red and violet fringes along the edges of a very brilliant white object seen against a white background.

281. **"Entoptic Phenomena."** — Furthermore, under appropriate conditions, a great variety of characteristic forms can appear in the subjective field of vision, in con-

sequence of anatomical structures within the eyes. These so-called " entoptic phenomena " are best observed when the eye is illuminated by means of a minute light source close to the pupil or, in some cases, impinging upon the sclerotic coat to one side of the pupil. They include floating spots, strings, stationary wrinkles, etc., which are due to dirt, mucus, or lachrymal formations on the surface of the cornea, cell *débris* in the aqueous and vitreous humors, or structural features of the lens. One of the best known appearances of this type is the so-called " snake-figure," which is determined by the shadows of the retinal blood vessels. (See Fig. 49.) This can be produced most easily by illumination of the sclerotic. Some individuals readily recognize the motions of the blood corpuscles within these vessels, when the eye is exposed to a uniformly bright area, such as the sky. Other retinal structures, including the yellow spot and the fovea, can yield entoptic effects under special circumstances.

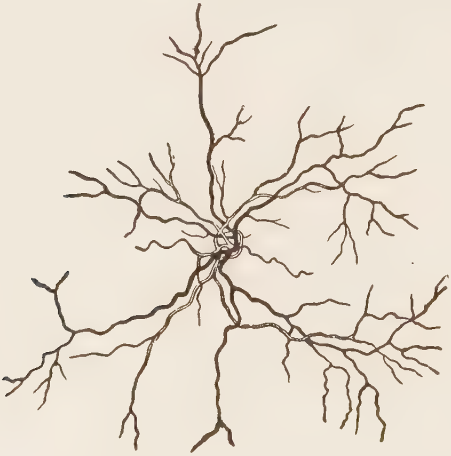


FIG. 49. THE RETINAL BLOOD VESSELS.

This drawing, taken from Helmholtz's *Physiological Optics*, shows the pattern of the blood vessels which intervene between the vitreous humor and the receptor cells of the retina, casting shadows upon the latter which may sometimes be seen as an entoptic "snake figure."

282. Field Functions. — The following facts may be noted concerning the part played by intraocular factors in the control of what we have called "field functions." First, as indicated in equation (10) above, the intensity of the retinal illumination decreases with increasing angle between a stimulus ray and the line of sight. This is to be attributed primarily to the decreasing area of the pupillary projection along the ray or line in question, but another influence of the same sort appears in the inclination of the retinal surface itself to the peripheral rays. The increased sizes of the interspaces between the peripheral receptor cells also operate in a similar direction. Owing to the fact, however, that, under dark adaptation, the periphery shows a much greater brilliance value, for a stimulus of constant intensity, than does the center of the visual field, we must suppose that these effects are more than counteracted by the sensitivity relations of the receptors. We must conclude, however, that such sensitivity differences between central and peripheral receptors, are actually greater with respect to the retinal image than as they are found from a comparison of the extraocular conditions, alone.

283. Pattern Functions. — Pattern functions also have obvious dependencies upon intraocular influences. In the case of stimuli of very small angular size, we may expect the blurring of the retinal image to bring about some confusion between intensive and areal characteristics. This will be the case, particularly, with objects, like stars, which are confined in an angle much narrower than that of a single receptor. Such objects are represented as having an appreciable area in the visual field. However, optical blurring effects will not suffice to explain the constancy of the energy threshold (intensity × area) for stimuli having diameters as great as 50 minutes of arc. They also fail to account for the way in which visual acuity is determined by intensity, since the relationship in question operates in a direction opposed to that of scattering or irradiation.

284. Acuity. — In general, we assume that acuity, or the limiting impression of doubleness in the visual field, must involve a certain degree of separation between adjacent illuminated retinal areas. Acuity will be lowered by all factors which favor lack of sharpness and lack of contrast in the retinal image. These include the various aberrations already mentioned above — spherical, chromatic and astigmatic — as well as numerous diffusive and diffractive effects. Such aberrations tend to increase with increasing size of the pupil. Failure to obtain satisfactory focus upon the retina, due to ametropia or other conditions, is also naturally prejudicial to good acuity. In order to arrive at a satisfactory understanding of the factors that underlie the visual representation of fine details, we must have recourse to a complete analysis of the optical resolving power of the eye; and we must not neglect the bearing of retinal and higher nervous center mechanisms. Hartridge[427] has made a very satisfactory study of the former problem, while the views of Hecht regarding the neurological basis of acuity will be considered below. (See page 132.)

285. **Temporal Functions.** — On account of the excessively minute span of time which is required for radiant energy to pass through the body of the eye, all of the temporal relationships of brilliance and the stimulus can be regarded as being independent of ocular optics. Their explanations are to be sought in receptoral and nerve conductional processes.

Section 56

MONOCULAR NEUROLOGICAL RELATIONS OF BRILLIANCE

286. **The Problem of Visual Theory.** — Following the logical course of our argument, we must now enter upon a discussion of the relationships between brilliance and the neurological factors in the visual afferent arc. These factors include the receptor mechanisms and processes, in the retinal rods and cones, together with conductional features

in the optic nerves and tracts. This domain of inquiry is classically designated as that of "the theory of vision." Theories, in this sense, are attempts to guess at the mechanism of the retina and its nervous appendages, along with the relations which exist between these factors and either consciousness or the stimulus. The theory of brilliance vision is properly regarded as a portion of the more general "theory of color vision."

We shall dispense, in the present analysis, with any detailed presentation of classical "color theories." The views of Helmholtz, Hering and Ladd-Franklin have received sufficient exposition in a multitude of papers and textbooks.[428] There are several hundred other hypotheses, not so popular but well worthy of study, which might also be reviewed in an historical discussion. However, practically all of these doctrines suffer from a failure to make contact with modern views concerning the nerve process. Such features as they may incorporate, which can be harmonized with recent demonstrations, we shall endeavor to consider in the appropriate contexts. It seems desirable to disregard the classical speculations, in the beginning, and to make a fresh start, along lines suggested by modern researches, especially those of Selig Hecht. We shall confine ourselves, in the present section, to the problem of brilliance, leaving chromatic aspects to be considered later. This procedure is justified by the seeming truth that brilliance vision is evolutionarily prior to the chromatic form, which is superimposed upon achromatic vision or differentiated from the latter.[429]

287. The Duplexity Theory. — However, we must pay homage to at least one classical theory, which has been so well substantiated that we can almost regard it as a fact rather than a theory. We have noted that there are two species of receptors, the rods and the cones, in the human retina. It was shown by Schultze [430] that, in certain lower animals, either rods or cones may be found in isolation. Animals which possess rods alone are essentially noctural in their habits, being blind in bright light; while those which are endowed only with cones are diurnal and night-blind. These observations immediately suggest that the rods are the organs of low intensity or *scotopic* vision, while the cones function for high intensity or *photopic* vision. This view may be designated as the *duplexity theory* (*Duplizitätstheorie*).[431]

The bulwarks of this theory lie in the numerous "explanations" which it affords for peculiarities of stimulus-experience relationships. We may consider, in the first place, the two visibility functions which characterize photopic and scotopic vision, respectively. The retinal rods contain a purple pigment, known as *rhodopsin,* or "visual purple." It is possible to extract this, by means of bile salts, and to determine its absorption spectrum. The latter is found to coincide very closely with the scotopic visibility curve, and it has been shown, furthermore, that rhodopsin is decomposed, or "bleached," by the action of light in accordance with the same curve. Consequently, we can hardly avoid the supposition that the decomposition in question lies at the basis of rod response and actually determines the form of the psychophysical scotopic visibility function.

We have already seen that the shape of the photopic visibility curve is practically identical with that of the scotopic one, although its position is shifted with respect to the latter, about 43 $m\mu$ along the wave-length scale. It has been suggested by Hecht[432] that rhodopsin is also the basis of cone response, and that the change in position of the curve can be explained upon the simple assumption that the general substance of the cones has a higher optical density than that of the rods. The familiar objection that the cones are apparently free from any pigment is readily met by pointing out the very low concentration of rhodopsin which would be required. The cones would need not more than one ten-thousandth part of the rod concentration, because their absolute sensitivity stands in this ratio to that of the rods. As a matter of fact, the requisite concentration of pigment in the cones would be even less than this since, in the case of the rods, the rhodopsin must act powerfully as an obstruction to the penetration of the receptor by the rays which are most effective in decomposing the pigment. The great rapidity with which the sensitivity of the cones changes under the influence of alterations in stimulus intensity, is another indication that only a relatively small quantity of sensitive substance is present. This same rapid change would make it almost impossible to detect the pigment by any ordinary method of objective examination.

The conformity of either of the visibility curves to a function of the probability type can be explained on the supposition that the individual molecules of rhodopsin vary from one another in accordance with a probability distribution. These variations may be permanent, but are more likely to be only temporary, depending upon dynamical considerations, such as the nature of their recent collisions with other molecules. Such differences would naturally be of a random character, but they would determine the susceptibility of the molecule to electromagnetic frequencies differing from those which characterize the typical, undisturbed, structure. The chances that a light ray will find a molecule which it can break up would, thus, decrease in accordance with a probability function, on either side of a maximum.

288. Facts Explained by the Duplexity Theory. — It should be obvious that these considerations furnish an " explanation " for phenomena which are correlated with the transition from photopic to scotopic vision, or *vice versa*. These include: (1) the Purkinje phenomenon, proper, (2) the analogous change which occurs when a stimulus pattern is moved from the center to the periphery of the visual field under dark adaptation, (3) the night-blindness of the fovea, (4) the low intensity inflexion of the acuity-intensity curve, (5) a similar inflexion in the flicker-intensity curve, and a number of other effects. In order to arrive at a full explanation of some of these phenomena, we must make certain further assumptions concerning the relative properties of rod and cone response. It is reasonable to suppose: (1) that the space detail resolving power of the cone system is much greater than is that of the rod system, and (2) that the response of the rods to a stimulus occurs much more slowly than does that of the cones.

The first supposition is practically necessitated by the spatial distributions of the two types of receptors, together with their characteristic nerve connections. At least in the center of the retina, the cones are packed very closely together, and each cone has its own conducting neurone. The rods, on the other hand, are separated by considerable interspaces, and are connected in groups to single nerve conductors. The peripheral cones also have group connections, but the groups are smaller than in the case of the rods. The relative sluggishness of rod response is rather more difficult to substantiate by purely physical evidence. However, the greater mass of rhodopsin which is involved, is suggestive of such a difference. We are also justified in regarding scotopic vision as a more primitive function than photopic vision, and for this reason the former might be expected to show a slower response than the latter. At any rate, there are a number of subjective phenomena which are explicable upon this assumption.

These phenomena include the change in the constants of the flicker-intensity law, at low intensities; the Purkinje after-image, and the so-called "fluttering-heart illusion." It is supposed that the Purkinje after-image rests upon the delayed response of the rods, with a moving stimulus, the primary image being attributable to the cone reaction. It is generally conceded that the after-image in question is absent or radically weakened in the center of vision, as would be expected if it is due to rod response. The "fluttering-heart illusion" consists in a relative motion of red figures against a blue background (or *vice versa*), viewed under twilight illumination, when the whole pattern is given an oscillatory movement. In this case, the failure of the rods to respond to the longer waves, together with their strong response to the shorter ones, is responsible for the illusion. The blue portion of the pattern lags behind the red portion, yielding the subjective effect of a relative motion between them. A similar phenomenon can be observed while driving an automobile at night, with the gaze fixed upon the road. If the latter is rough, the rocking of the car seems to induce an oscillatory displacement of the illuminated dashboard with respect to the windshield. In this case, the effect is due to the predominance of rod vision in the periphery of the visual field, as compared with the center.

289. Fundamental Photochemical Relationships. — The action of radiant energy upon the retinal rods and cones almost certainly consists in the chemical decomposition of a "photosensitive" substance. Now, *photochemical* processes are subject to well-established principles, and can be treated quantitatively upon a theoretical basis. The investigations of Hecht,[433] Lasareff [434] and the writer have shown that these principles are capable of accounting quite accurately for numerous psychophysiological relationships.

The simplest possible assumption regarding the initial action of the stimulus upon the retinal rods or cones seems to be that a certain substance, S, is decomposed into two other substances, which Hecht designates as P and A. This reaction may conceivably be either reversible or irreversible. In the former case, P and A recombine freely to reconstitute S, but, in the latter case, S must be resupplied by nutritive or general metabolic processes. There is also the possible compromise of a so-called pseudoreversible relationship, in which one of the decomposition products (say A) combines with a freshly supplied substance to regenerate S. For reasons which we shall consider below, this last type of reaction appears to be the most likely one for the photosensitive process involved in vision. The process by which S is generated, originally, is reversible and bimolecular, and so also is that of its decomposition under the influence of the stimulus, but the two reactions are not identical.[435]

Now, it has commonly been assumed that the *rate* or "velocity" of the reaction:

$$S \rightleftharpoons P + A, \tag{11}$$

from left to right, is correlated positively with the degree of brilliance in the visual field. If we represent the concentration of P by x, this velocity can be written as dx/dt. However, it is necessary to introduce some intermediate links, to explain how the intensity of the chemical change can be reflected in the activity of the optic nerve fibres. Here, the simplest supposition seems to be that one or both of the end-products, A and P, act as nerve excitants, whereas S is ineffective in this regard. The intensity of the nerve action would thus be a function of the concentration (say) of P at any moment, and this would depend upon the rate at which P is being formed.

Hecht believes that it is necessary, at least for the light responses of molluscs, to introduce a *secondary chemical reaction,* $L \rightarrow T$ which is catalyzed by the end-products of the primary reaction. In this case, the concentration of T is responsible for the degree of neural activity. He finds it reasonable to suppose that the velocity of the secondary reaction is proportional at any time to the concentration of the end-products of the primary change. Although such a mechanism seems rather complicated, it is in harmony, not only with Hecht's observations on the latent period, but with the extreme absolute sensitivity of the retina, which, as we have seen, is about three hundred thousand times as great as that of the best modern radiometer. The secondary reaction is presumably irreversible, or it would not be usefully amenable to catalytic encouragement. In this case, we must assume a very efficient means for the elimination of T. We shall discuss the interpretation of this secondary process again, below.

290. **The Reciprocity Law.** — Probably the most fundamental law, which is applicable to photochemical reactions, is the well-known reciprocity or Bunsen-Roscoe principle. According to this generalization, the total photochemical effect (the amount of substance which is decomposed) is dependent upon the product of the intensity and the time, these two variables being metrically interchangeable. In the visual instance, it is reasonable to suppose that the production of a threshold degree of brilliance, with brief exposures, corresponds to the generation of a fixed amount

of *P* or *A*. In combination with the reciprocity principle, this assumption explains the constancy of the exposure threshold, for short times of stimulus action.[436] It also lies at the basis of the Talbot-Plateau law (*q.v.*). When the times are long or the intensities too high, relatively to the times, deviations from constancy are to be expected due to such factors as exhaustion and diffusion. With extremely short times, deviations are also to be expected, as in the case of photographic exposures. Within limits, however, it seems that the generation of a constant amount of end-product, *P*, yields a fixed brilliance, or brilliance increment, in consciousness. It appears, also, from the work of Lasareff,[437] that the amount of energy which must be absorbed by the photosensitive substances, for a fixed brilliance result, is constant, regardless of the stimulus wave-length. The variation in the threshold, with change in wave-length, is attributable to an alteration in the efficiency of absorption, rather than to any change in the requisite amount of photochemical effect.

291. The Photochemistry of Adaptation. — *Dark Adaptation.* — The general laws of both photopic and scotopic adaptation can be accounted for on the basis of simple photochemical assumptions. Thus, Hecht [438] has shown that the functions which connect threshold intensity with time, for either rod or cone vision, conform to the temporal law of a bimolecular reaction. (See Fig. 50.) He supposes that the end-products, *P* and *A*, recombine in the dark to reconstitute *S*. It seems doubtful, however, whether the two "precursors" of *S*, in this process, can be identical with its photochemical decomposition products. At least one of these precursors is probably supplied afresh from the retinal pigmentary epithelium. It has been shown that rhodopsin is reconstituted, after bleaching by light, only under special conditions, particularly when contact is maintained between the receptors and the pigmentary tissue.

The relative slowness of the process is also inconsistent with an identification of the entire mass of the dark adaptation precursors with decomposition end-products. Hecht's studies show that the velocity constant of photopic dark adaptation is much higher than that for the corresponding scotopic process, while the change in concentration is much less. The general form of the equation which is involved is:

$$k = \frac{1}{at}\,\frac{x}{a - x} \tag{12}$$

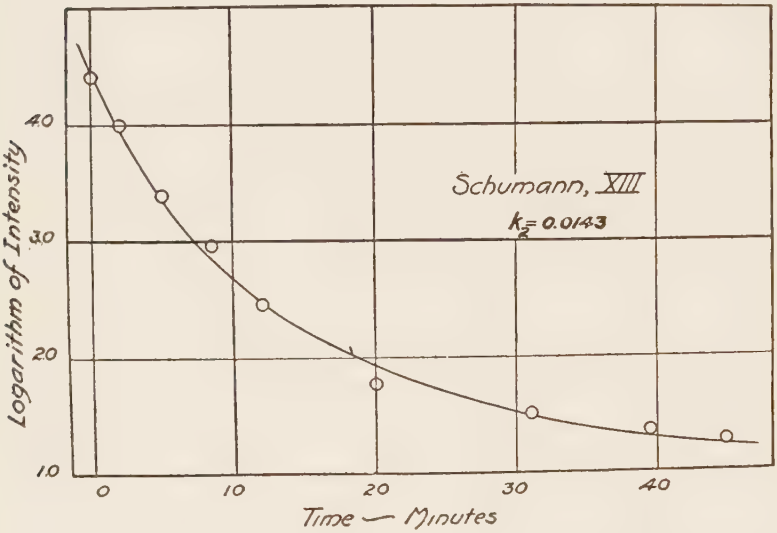


FIG. 50. THE COURSE OF DARK ADAPTATION IN THE HUMAN EYE.

This curve, due to Hecht, shows how the light intensity required for threshold stimulation of the retina alters as a function of the time after the eye is first exposed to darkness. The curve itself is computed from the equation for a bimolecular reaction, while the circles represent the experimental data of Piper.

where k is the velocity constant, x the concentration of one of the precursors at the time, t, and a is the final concentration of S. For scotopic dark adaptation, k has a value of about 0.016, when t is expressed in minutes. The corresponding constant for photopic dark adaptation is 0.162. Thus, the facts are consistent, in general, with the assumptions of the duplexity theory.

Bright Adaptation. — The process of "bright adaptation" to any given stimulus intensity, I, can also be treated in an adequate manner. Hecht[439] assumes, in harmony with familiar photochemical principles, that the rate of decomposition of S, dx/dt, is proportional to the intensity and to the given concentration of S, thus:

$$\frac{dx}{dt} = k_1 I(a - x), \tag{13}$$

x being the concentration of P or A at the given instant, and a the original or limiting concentration of S. As soon as x is greater than zero, a process of recombination sets in, following the equation:

$$-\frac{dx}{dt} = k_2 x^2. \tag{14}$$

The first reaction must evidently decrease in speed, with time, while the second must increase, so that eventually they will become equal and opposite, producing a so-called "stationary state," in which

$$I\frac{k_1}{k_2} = \frac{x^2}{a - x} \tag{15}$$

In this relationship, the sensitivity may be considered as represented by the expression, $a - x$, or inversely, by x. It is apparently lower, the higher the intensity, I, of the stimulus, in accordance with an equilibrium which is determined automatically by the magnitude of I. This corresponds to the "allonomous equilibrium" of the Hering theory, and received mathematical representation in a photo-chemical theory of sensory response which I published fifteen years ago.[416]

Hecht treats the sensitivity as being primarily dependent upon the concentrations of P and A, rather than that of S, which seems the more natural assumption. In the case of the clam, adaptation to any intensity yields complete cessation of response, and experiment shows that the same increase in the value of x is required to elicit a reaction, regardless of the adaptation level. This means that a constant amount of chemical decomposition must be added to that already established, as if the nervous system of the animal had neutralized the existent effects of P and A in their given concentrations. However, in human vision, the neutralization — if it be such — is generally incomplete at equilibrium, since, ordinarily, there is a permanent enhancement of the brilliance.

292. **Receptor Basis of the Fechner Relationship.** — I have shown that the general form of the Fechner function can be explained on the basis of two rather different sets of assumptions regarding retinal chemistry. Hecht[440] has also arrived at similar results on still another basis. All of these methods of reasoning yield a function which is approximately logarithmic over a middle range of intensities, but which involves an increase in the relative threshold, $\Delta I/I$, at lower and higher intensities. Hecht has shown that if we assume the equation, $k_1 I/k_2 = x^2/(a - x)$, to hold for the human retina, a constant increment or decrement of x is required to yield a just noticeable difference in brilliance, when the eye is in equilibrium with the intensity, I. Such equilibrium exists, at least approximately, under ordinary conditions of visual experimentation, as employed by König and Brodhun in their determination of the Fechner function. On the basis of their data, Hecht finds $k_1/k_2 = 100$ for the scotopic region, and $k_1/k_2 = 0.25$ for the photopic region, the constancy of Δx being restricted to the respective intensity ranges. The condition for brilliance discrimination in the human nervous system is thus identical with that for photic reaction in the mollusc. In both cases, the relative threshold in terms of stimulus intensity, $\Delta I/I$, is not constant, but shows a minimum in the medium intensity region.

293. **The Mechanism of Optic Nerve Excitation.** — In order to clarify our view of retinal psychophysiology further, we must form a somewhat more precise picture of the relationship between the photochemical processes and the excitation of the optic nerve fibres. The problem is a rather definite one in the light of our modern knowledge of the

neural process. We must show how the quantitative aspects of the photochemical reactions can be translated metrically into variations in impulse frequency in the conducting neurones. The simplest hypothesis, in this situation, appears to be the one which we have already outlined in our general discussion of receptor action. (See page 43, above.) It involves the idea that the process, $S \rightarrow P + A$, is one of ionization. This view is particularly appealing because, firstly, the electromagnetic forces of the stimulus should be expected to produce exactly this effect and, secondly, an ionization increase readily permits us to understand how the concentration of photochemical end-products can control the nerve pulse frequency. However, we have no evidence that the action of light upon rhodopsin causes ionization, and the secondary reaction, $L \rightarrow T$, of Hecht's theory seems to lack an interpretation in the ionic hypothesis.

Interpretation of the Secondary Process.—Hecht himself has suggested that this secondary process might be physical (diffusion) rather than chemical, although in the clam, its temperature coefficient seems to enforce the latter interpretation. However, Adrian and Matthews[441] find that, in the eel's eye the secondary process cannot be one of catalysis, because its locus differs from that of the primary process. Now, considerable difficulty seems to attach to Hecht's conception of the secondary reaction, in its application to the human eye, because of its metabolic requirements. It is evidently not a reversible process, but it would seem that its end-products must be capable of very rapid elimination. In general, some such interval as a tenth of a second suffices to reduce the brilliance to the level of the idio-retinal light after the removal of a stimulus, and this could not occur if any appreciable increment of T remained at the end of this time. Evidently, we have the further requirement that large quantities of L should be available to maintain this rapid, destructive process.

It appears, in the light of these considerations, that the most satisfactory interpretation of the secondary process is as follows: The primary reaction, $S \rightarrow P + A$, generates a substance, *P,* which is capable of reacting with the membrane surrounding the receptor cell, so as to excite, or to increase the excitability of, the latter. The secondary process involves two phases, first, the diffusion of *P* to and into the membrane and, second, its reaction with the membrane. This reaction may well be describable in chemical terms, and have a temperature coefficient similar to that found by Hecht. It is entirely conceivable that the effect of *P* upon the membrane should follow catalytic principles. At any rate, we may assume that its action is such as to increase the permeability at a rate which is proportional to its concentration. This will bring about excitation in a time which is inversely proportional to the concentration, as demanded by the experimental findings. The secondary reaction is thus not the production of an excitant, but rather the production of excitation. It is well known that the time required to excite a nerve varies inversely as the intensity of the exciting force.

This interpretation of the secondary process removes the difficulties regarding metabolism and continued excitation which we have noted above. The substance, *L,* may be identified with some aspect of the membrane structure itself, while *T* represents the excited state of this structure, or, at any rate, the increased permeability which sets off the impulse. The reaction, $L \rightarrow T$, is reversed when the membrane is rebuilt during relative refractory phase, but this process requires the expenditure of oxidative energies, and hence reagents which are in addition to *L* and *P*. It is reasonable to suppose that the moiety of *P* which has reacted with the membrane is chemically destroyed during excitation and recovery, so that it is eliminated from the system altogether. Furthermore, it seems inevitable that a certain amount of *S, P* and *A* should be lost by diffusion out of the cell during the phase of high permeability which accompanies excitation. These losses must be compensated by the counter-diffusion of replenishment substances into the cell, and the exact status of the equilibrium between these various influences must rest upon rather complex mechanisms of metabolic regulation, and be subject to minor accidental disturbances.

Basis of the Idio-Retinal Light. — If the stimulus remains in operation, a certain concentration of P will be maintained, and the excitation of the membrane will therefore be continued, at a rate which is roughly proportional to the concentration in question. When the cell recovers from refractory phase it is again subjected to excitatory action. However, if the stimulus is removed, there must be a practically instantaneous reversal of the reaction, in the sense, $P + A \rightarrow S$, so that the concentration of P is quickly reduced to its normal, unstimulated value, or below. The existence of the idio-retinal light leads us to suppose that a certain amount of decomposition may occur spontaneously, so that there is a constant slow flow of impulses along the optic nerve fibres. In the absence of this assumption, it seems difficult to explain the possibility of negative after-images which are darker than the idio-retinal brilliance. The assumption would take the mathematical form of

$$(16) \qquad \frac{dx}{dt} = k_1 I(a - x) + k_3(a - x),$$

in Hecht's notation, where k_3 is the constant of self-excitation. In the absence of a stimulus, or $I = O$, we should have an autonomous equilibrium, governed by the relationship,

$$(17) \qquad \frac{k_3}{k_2} = \frac{x^2}{(a - x)}.$$

Other Possibilities. — The above development of Hecht's views amounts to a rejection of his idea that the processes which underlie adaptation are substantially identical with those accompanying excitation. It seems that the velocity constants of the former are too low to permit them to meet the demands of the excitatory process, at least in the human visual system. It appears that we must assume, virtually, that P is used up, in producing excitation, at a rate comparable with that at which it is generated, the latter depending upon the concentration of S. The regeneration of S is determined by A and a substance which is supplied afresh. A pseudoreversible system, of the type suggested by Hecht, involving three precursors of S and three decomposition products, will probably meet all of the elementary requirements. Two of the precursors are identical with two of the end-products; the other precursor is present in great excess, while the additional end-product is used up in producing excitation.

Another possibility, which is more directly in line with Hecht's thought, is as follows: The system is actually limited to S, P and A, together with the membrane, and the reaction, $S \leftrightarrows P + A$, is of the slow type which characterizes the adaptation processes. However, the membrane adapts itself to the concentration of the end-products, so as to maintain itself, as nearly as possible, in an unexcited condition. This membrane adaptation would follow the same laws as do electrotonic changes in excitability. (See page 29, above.) An increase in the end-product concentration would then be required to elicit nerve fibre response, and such a differential change could occur much more rapidly than would be characteristic of the total range of the photochemical reaction. This view, however, encounters serious difficulties in its application to human vision, because it does not permit of sufficiently sustained response, nor of a depression of the response below the idio-retinal level.

294. The Representation of Brilliance in the Optic Nerve Process. — We are led by the above considerations to the general notion that the subjective degree of brilliance is correlated with the frequency of the impulses which pass along the individual fibres of the optic nerve. The brilliance at any point in the visual field would thus be determined by the impulse frequency in the corresponding fibre. The existence of a pulsatory current in the optic nerve, when the retina is stimulated by light, is proven by objective tests, as in the experiments of Adrian and Matthews.

The "Blue-Arc" Phenomenon. — There is also an interesting entoptic effect, known as the "blue-arc phenomenon," which presents indirect evidence as to the all-or-none character of the optic fibre impulses. This phenomenon consists of momentary flashes of violet-white luminescence in the visual field, accompanying the exposure of the central region of the retina to a stimulus of limited area. The contours of these flashes follow the course of the retinal nerve fibres from the stimulated area to the exit of the optic nerve, so that we may reasonably suppose that they are due to the excitation of the retina adjacent to the course of the fibres, by the action currents in the latter. My measurements [442] show that the brilliance of the arcs is substantially independent of the intensity and the wave-length of the original stimulus, as would be expected if they are determined by the voltage amplitude of the unit all-or-none nerve pulse.

It is, furthermore, of interest that the brilliance of the arcs is very close to that which is given by a stimulus just above the absolute threshold, in dark adapted scotopic vision. The probable mechanism of their production suggests that they involve the generation of a single added impulse in each nerve path which is concerned. Presumably, they are referable to electrical excitation of the receptors which are adjacent to the active conducting paths, and such excitation is apt to involve a single impulse, in accordance with Du Bois-Reymond's principle. In this case, we should be justified in attributing the so-called absolute threshold to a single impulse per fibre, when the simultaneous activity of a considerable number of adjacent fibres is involved.

The question as to the exact quantitative nature of the function which associates nerve impulse frequency with brilliance, when the latter is measured on a scale determined by just noticeable differences, is of great interest. Is it likely that the two variables are exactly proportional? The pertinent experimental data, so far as they go, indicate an affirmative answer. It is quite certain that the nerve current stands in a Fechnerian relationship to the stimulus intensity. As we have seen, this sort of a function holds between the stimulus and the photochemical effect. It has also been demonstrated by Chaffee and Bovie,[443] and other investigators, for the action current of the retina in excised eyes. Such measurements probably involve the number of coöperating units as well as the impulse frequency, but it appears almost certain that the original doctrine of Fechner, that the logarithmic relationship holds between the psychical variable and the direct determinant in the cortex, is not true. The logarithm of a logarithm is not a logarithm.

295. Multifibral Correlations of Brilliance. — However, the problem of the neurological relationships of brilliance is not to be solved completely by considerations bearing upon processes in single nerve fibres or receptors. The insulation between adjacent processes is perhaps greater in the visual system than in any other neuropsychic domain, but it is far from being perfect. Within the conducting tracts proper, of course, there is presumably no appreciable cross action, but in the synaptic layers of the retina and the cortex, this is not the case. We may note, in the first place, that only in the foveal region is each receptor provided with a "private" nerve conductional line. Where a number of receptors are connected to a single conducting neurone, the intensity of the current in the latter is presumably determined by the combined action of all of its attached sense-cells. However, even in the center of vision, there is an overlap of process between adjacent points.

Such an interaction or coöperation of adjoining visual elements appears, particularly, in the principle of the constancy of the threshold in terms of intensity and area, for small areas; and in the continued dependency of the intensity threshold upon area, for larger areas. It is also demonstrated in the function which relates acuity and intensity. Contrast involves a reciprocal influence between the activities in adjacent regions.

296. Hecht's Theory of the Acuity-Intensity Law. — The acuity-intensity relationship has recently been made the object of a very fruitful study by Hecht,[444] who computes that, at the lowest intensities, the minimal visible involves a foveal area which contains no less than 540 cones. As the intensity is raised, this area diminishes, until it corresponds to the diameter of a single cone. Hecht supposes that the thresholds of the individual receptors differ from one another, in a manner describable by means of a probability distribution curve. (See Fig. 51.) At low intensities, the available receptors are sparsely distributed in the retinal field, but, as the intensity increases, the excitable units become more numerous and hence more closely packed. At the limit of acuity increase, the total assembly of receptors is available and such packing is at a maximum. The basis of the acuity-intensity law is thus assimilated to that of a photographic emulsion, having a resolving power which depends upon the size and spacing of its component grains. In the case of the retina, the increase in grain fineness with

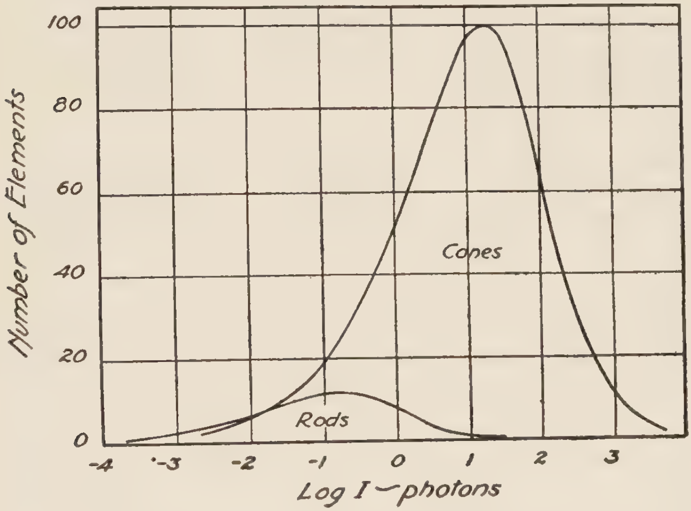


Fig. 51. Distribution of Thresholds Required to Explain the Data of Visual Acuity, According to Hecht's Theory.

The ordinates of the curve show the number of rods or cones having their absolute thresholds at intensities shown by the abscissae. In reading this curve, it should be noted that Hecht's use of the "photon" is in error by being based upon millilamberts instead of upon candles per square meter. Consequently, his intensity values should be multiplied by 3.183.

intensity is functional rather than structural, but the result is the same.

Hecht finds that the distribution of thresholds with respect to stimulus intensity can be divided into two more or less skewed probability functions, having characteristic constants, and corresponding to rod and cone response, respectively. The transition from scotopic to photopic vision occurs at an intensity where only half of the rods are excited. The number of rods included in the minimum visible area, at the lowest intensity, is about sixty, or only about 1/9th the number of cones. It is interesting that the maximal scotopic acuity should also turn out to be about 1/9th the best photopic acuity. The same fraction applies to the relative amounts of photochemical change required to yield brilliance discrimination in the respective systems. This may be due to the fact that such discrimination involves the number of receptors in a " unit area " along with the degree of excitation of these receptors. Such an interpretation would evidently imply that the threshold photochemical change is the same for each species of sense-cells, corresponding to the same change in nerve pulse frequency, and an identical discrimination mechanism in the cortex, operating upon the nerve currents independently of their receptoral origin.

297. **General Implications of Hecht's Theory.** — If we accept the implications of Hecht's analysis, it follows that, in vision with large areas at low intensities, relatively few receptors and nerve paths are involved. In spite of this, the subjective impression is one of uniform brilliance over the corresponding part of the visual field. At higher intensities, there is a much greater restriction of process. Hence, it may appear that the principle of diffusion of excitation, here, is the reverse of that which characterizes simple physical processes, in which the diffusion is greater the higher the intensity. However, it is likely that, in the recognition of variations of brilliance with respect to position, we have to do with a discrimination mechanism which is affected by the absolute excitation gradient. The gradient

between the idio-retinal excitation and excitations which are just over the absolute threshold may be too low to permit a judgment, except under the condition that the space factor is increased beyond the range of the internal irregularities of the excited area. The influence of "contrast" is also undoubtedly involved. We shall have more to say concerning the details of these relationships in our discussion of cerebration. (See Volume III.)

When we are studying the processes which go with increasing brilliance on a considerable area, we probably have to deal with an irregular constellation of excited receptors and nerve fibres, some of which are operating at minimal frequency, while others are functioning at various higher frequencies. The whole system, however, is ironed out into effective uniformity in the cortex, on the basis of some kind of averaging arrangement. The cortex must involve processes of summation, persistence, and dispersion, which probably cannot be formulated wholly in terms of ordinary nerve excitation, but rest upon the behavior of excitatory and possibly inhibitory substances, such as the symbolic E and I, which we have considered in a previous section. (See page 50.)

Hecht finds that the number of cones, 540, in his so-called "unit retinal area" is equal to the total number of just noticeably different steps in brilliance, from the lowest to the highest values of the latter, if we subtract the number of steps which are attributable to the rods only. The significance of this coincidence is rather dubious. It would seem to imply that if we start with a unit retinal area at the absolute threshold, each time a single cone is added to the excitation system, there will be a just noticeable increase in brilliance. As a matter of fact, there will be simultaneous increases in frequency, as we have noted and as Hecht himself recognizes. It is unlikely that the total number of just noticeably different brilliance steps corresponds to any fixed constellation of anatomical or physiological units. There seems to be no reason why a threshold change in brilliance should correspond to a unit impulse per arbitrary unit of time, or even that it should go with the addition of a unit conductor. Moreover, it is notorious that the differential threshold varies widely in a fixed intensity range as a function of surrounding conditions, such as the sharpness of the demarcation lines between the two areas which have to be discriminated, concomitant color differences, and the like. König's differential thresholds (used by Hecht) were unusually high, at their lowest, corresponding to a Fechner fraction of about 0.0150, to be compared for example with 0.0067, reported by Helmholtz. Nevertheless, a precise determination of the quantitative relations which are involved in this situation is of the utmost interest. Perhaps it should include a study of the phenomenal characteristics of small stimulus areas at low intensities.

298. **Retinal Causes of Contrast.** — It seems likely that the major facts of contrast are attributable to cortical activities. However, there are certain processes, to be expected in the retina, which should yield contrast effects. We have already noted that, when the receptor cells are excited, there is presumably a loss of excitation end-products into the surrounding tissues. Now, these tissues embrace other receptor cells which may be at a lower state of excitation. The end-products from the more strongly active receptors may be expected to penetrate the less active receptors, and to influence the course of their photochemical processes. If, as we have assumed, the excitatory substance, P, is largely consumed in the process of excitation, the substance, A, will be the end-product which is primarily involved in this process of diffusion. In accordance with the principles of chemical mass action, its accumulation in the receptors will encourage reversal of the photochemical change, and will tend to decrease the concentration of the excitatory substance, P. The consequence will be a reduction in the nerve currents which are aroused by the less strongly stimulated receptors. A similar action will, of course, occur between receptor areas which are equally stimulated, but in this case it will merely bring about a general depression of activity, not distinguishable from adaptation. It is likely that con-

trast effects based upon the mechanism in question will be limited to rather small distances in the visual field or will require considerable time to develop. Consequently, they should presumably be used to explain edge effects, halos, etc., rather than large areal interactions.

299. Temporal Phenomena and Visual Diffusivity. — It is evident that, although changes in the stimulus may be practically instantaneous, the retinal and nerve conductional processes must have an appreciable inertia. The primary photochemical change requires time in order to produce any finite amount of end-product, P, and the secondary reaction extends the latent period even farther. When the stimulus is cut off, the reversal of the chemical condition or the subsidence of the excitation, must occupy a considerable fraction of a second. The conductional and, more particularly, the cortical processes must also possess important inertia properties. In the case of the optic nerve fibres, however, the temporal lag must be limited essentially to the duration of a single conductional impulse, which may be only a thousandth of a second. The condition following the impulse, *per se,* tends to be refractory rather than a continuation of excitation. In the cortex, on the other hand, we may expect to find a definite cumulative effect. Reference should be had to many papers by Piéron [445] for a detailed analysis of the numerous factors which are involved in reaction or response time.

In studying the laws which govern flicker, H. E. Ives [446] has found it helpful to draw a parallel between the visual process and that of conduction by diffusion or radiation. An action of the latter sort is exemplified by an electric lamp filament which may be heated by a fluctuating current. The heat capacity of the filament tends to minimize and to smooth the current variations, but this effect will be less in proportion as the heat dissipating power of the filament is greater. The process is formulated by Fourier's equation, according to which

$$\frac{d^2V}{dX^2} = \frac{1}{k}\frac{dV}{dt}, \tag{18}$$

which states that the rate of change of the given potential, V, is proportional to the first space derivative of its gradient. The constant, k, is known as the diffusivity. It seems hardly possible to follow Ives' implication that the visual propagation itself is actually diffusive, but this interpretation is not essential to his reasoning. It is sufficient to recognize that, in systems of sensory or neural excitation, we are probably dealing with local accumulations of some sort which tend to be dissipated in accordance with Fourier's equation. It is more probable that this action occurs either in the receptor cells or in the cortex than in the main conduction channels, where the process is essentially non-dissipative.

The general way in which this smoothing action accounts for the persistence of vision should be obvious. Ives' detailed applications of the diffusivity idea, to the relations between the flicker photometer and critical flicker frequency values, yield results in such striking conformity with the facts that we cannot doubt the fundamental importance of the concept. He finds that the diffusivity coefficient increases as the logarithm of the stimulus intensity, being somewhat greater (especially at low intensities) for long-wave than for short-wave radiation, at the same photometric value. Analysis indicates that, for single stimulus pulses, the interval between the moments of application and of conscious representation (latent period) should be inversely proportional to the diffusivity. Ives has shown that dim lights do in fact lag behind bright ones, and that red and blue at equal brilliance show the relative latent periods which are demanded by their flicker behavior. The most likely supposition is that these latent period effects are conditioned by the velocity of the secondary reaction in Hecht's scheme. These considerations would seem to apply to the alleged differences in rate of rise of equally brilliant colors of different hues. We shall consider their significance in greater detail in our discussion of chromatic problems.

300. The Significance of Charpentier's Bands. — The phenomena known as Charpentier's bands are highly suggestive of the pulsatory character of the nerve conductional process, as demanded by the all-or-none theory. The time characteristics of these bands corresponds to a frequency in the neighborhood of forty per second, which is not an unreasonable value for low degrees of retinal excitation. Direct measurements upon the eyes of animals have shown impulse frequencies of this order of magnitude. Moreover, the bands increase in number per second with augmented stimulus intensity. McDougall[447] reports that the leading band, corresponding to the initial action of the stimulus, is brighter than the others, which fade in brilliance more or less progressively. It would seem that if each band represents a single all-or-none pulse, they should all be of the same brilliance, but it is highly probable that the leading band involves the superposition or overlap of a considerable number of unit impulses. It is legitimate to suppose that a single pulse has a definite brilliance value and that increases above this are referable to cortical summation. Evidently, the majority of the bands are due to residual excitation which continues after the removal of the stimulus.

Section 57

MONOCULAR STIMULUS RELATIONS OF CHROMA

301. Statement of the Problem. — In our discussion of the introspective properties of colors, we have employed the word, *chroma,* substantively, to designate those colors which exhibit hue and, hence, saturation. The term may also be used to stand for the combination of hue and saturation, regarded as chromatic attributes of color, in contradistinction to brilliance, the achromatic attribute. In this latter sense, chroma is synonymous with "quality," as this word is frequently employed to represent the non-intensive aspects of color. This usage of the term, chroma, should not be confused with Titchener's[448] use, which makes it the equivalent of what we have called *saturation.*

A study of the psychological color solid, as presented in Note A (page 354 below), reveals the intimate relationship which exists between hue and saturation, in accordance with which saturation can be regarded as measuring the intensity or amount of hue. In order that a color should exhibit hue it must possess a definite degree of saturation greater than zero, the saturation indicating the extent to which it differs from the gray of the same brilliance. Conversely, there can be no saturation without the presence of some definite hue, and the hues are all mutually exclusive. This last statement is not inconsistent with the notion of psychologically primary hues, red, yellow, green and blue, which occupy salient points on the color circle, and of intermediate hues, which can be described in terms of their peculiar resemblances to their psychologically primary neighbors on either side.

The problem which we now face is that of specifying the relationships or functional dependencies that associate hue and saturation, on the psychological side, with variables which determine them, on the physiological or physical side. These latter variables are approximately the same ones which we have considered above as determinants of brilliance, although the laws through which they control the chromatic attributes of color differ radically, in many cases, from those which are involved in the psychophysics of brilliance. In other cases, the chromatic and achromatic relationships present striking similarities. The chromatic phenomena vary widely with position in the visual field, and we shall consider, primarily, the laws which govern them in the central or foveal region.

I. CHROMA AND WAVE-LENGTH

302. Naming the Spectral Chromas. — Hue is ordinarily regarded as an index of the wave-length, or at least of the "dominant wave-length," of the stimulus, just as brilliance is usually considered to be indicative of the stimulus intensity. Careful experimental studies, however, show that the dependencies of hue upon stimulus and retinal characteristics are extremely complex, and can ultimately be understood only in terms of a physiological, rather than an external physical, theory. If we excite the retina by projecting upon it a physical spectrum, which consists of a series of substantially homogeneous or pure wave-lengths, experience reveals a series of colors having, in general, high saturation and varying radically in hue. Under normal conditions, the hues range from a slightly yellowish red, at one end of the spectrum, through orange, yellow, yellow-green, green, blue-green, blue, to violet (a reddish-blue), at the other end. This is exactly the order of the given hues in the *color cycle* of the introspectively constructed psychological color solid, the constitution of which has in itself absolutely nothing to do with the physical spectrum. In the *color spectrum, i.e.*, the series of colors normally evoked when the physical spectrum is employed as a stimulus, however, the cycle of hues is incomplete, on account of a gap between the two spectral extremities. In this gap lie the purples and the true, psychologically primary, red.

The most primitive way in which to establish a relationship between hue and wave-length is to assign *names* to the spectral colors, and then to determine the wave-length ranges corresponding to the designated qualities. Thus Newton divided the spectrum into seven colors, and later investigators have suggested other methods of subdivision. These schemes, however, are of little interest at the present time, since we must recognize that there is a continuous variation of chroma throughout the spectrum, and that the only individual colors which can be discriminated therein are those separated by just noticeable or liminal chromatic differences. There are not seven of these, but approximately one hundred and thirty. It must be recognized, furthermore, that the simultaneous observation of the complete spectrum introduces contrast conditions which are unfavorable to the determination of normal relationships between chroma and wave-length.[1] Under these contrast conditions, the separation of the colors into distinct bands is much sharper than is indicated by the normal relationships. Such an exaggerated separation — into only three colors — is particularly sharp in a so-called subtractive spectrum, which is produced by forming a spectrum of a dark line on a bright background, instead of a light line on a dark background as is the practice with the ordinary or so-called additive spectrum. The most significant way in which to establish boundaries inside of the color spectrum is to locate the psychologically primary hues, at definite points within it. Of these the red is absent, but the yellow, green and blue are situated, according to the data of Westphal,[449] at 574.5 $m\mu$, 505.5 $m\mu$, and 478.5 $m\mu$ respectively. These figures hold, of course, only for the average normal observer under normal conditions. Chromatic adaptation and partial color-blindness shift these positions radically.

303. The Spectral Chroma Scale. — Although the stimuli, provided by the physical spectrum, are of substantially maximal purity, this is no guarantee that the corresponding colors are of maximal or even equal *saturation.* Indeed, a direct comparison of the spectral colors indicates clearly that their saturations vary to a marked degree. Hence the manner in which pure hue depends upon wave-length cannot be ascertained by utilizing spectral or homogeneous stimuli alone. Nevertheless, it is of great interest to know how the scale of chromas actually presented in the spectrum varies, simultaneously in hue and saturation, as a function of wave-length. Careful determinations of this function, which indicates our ability to discriminate differences in wave-length in various regions of the spectrum, have been made by König,[396] Steindler,[450] Jones,[451] and Laurens [452] for normal, and also for color-blind, observers. Although these investigators have regarded their results as establishing a scale of pure hue, the scale in question must, in strictness, be called the *spectral chroma scale.*

Jones finds 128 just noticeably different chromas through the spectrum. If these are numbered in order, beginning at the red (as shown in Table VII), they can be plotted with respect to wave-length to yield the curve given in Fig. 52. Since this curve is not a straight line, the wave-length difference required to produce a liminal chromatic difference must vary as a function of wave-length. This latter function, which may be regarded as the first derivative (or law controlling the slope) of the function represented in Fig. 52, is depicted in Fig. 53. It will be noted that the wave-length discrimination threshold — in the ordinates of Fig. 53 — shows distinct minima at 440, 492, 581, and 635 $m\mu$ respectively, the lowest thresholds lying in the yellow and the blue-green where a difference of 1.0 $m\mu$ can be detected. The wave-length discrimination threshold is obviously inversely proportional to the sensibility to differences in wave-length. It is furthermore to be noted that, at either end of

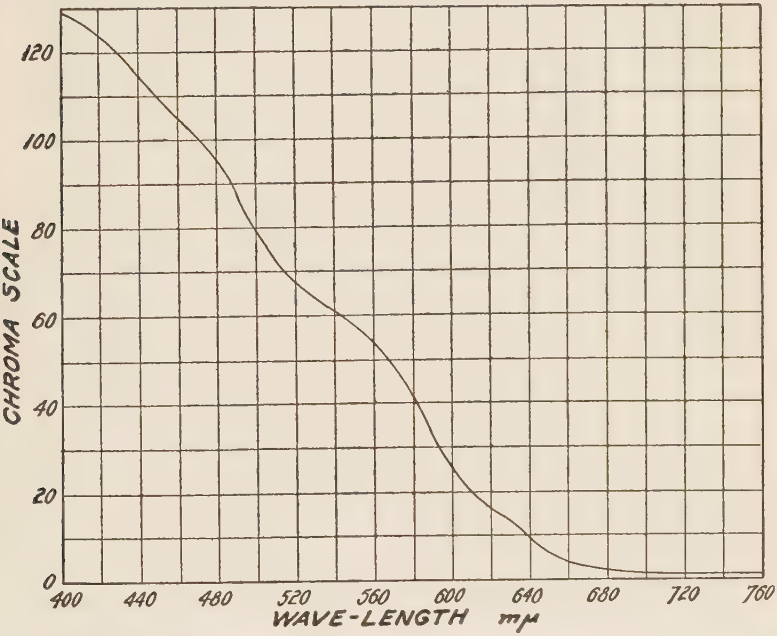


FIG. 52. THE DEPENDENCY OF SPECTRAL CHROMA UPON WAVE-LENGTH.

This curve has been produced by plotting the chroma scale numbers of Table VII against the corresponding wave-lengths. It will be seen that the chroma changes fairly steadily with wave-length, except at the extreme long-wave end of the spectrum.

the spectrum, the sensibility becomes very low, there being no change in chroma between the extreme long-wave end of the spectrum and a color corresponding to 670 *mμ;* with a similar but shorter range in the violet.

It is of interest to note the positions of the psychological primaries in the spectral chroma scale. The red, of course, is not included, but the blue, green, and yellow lie at Nos. 96, 75, and 45 respectively. Their spacing is evidently quite irregular, but our failure to perceive a law may be due to the combination of saturation variations with those of hue, as well as to the absence of the red primary.

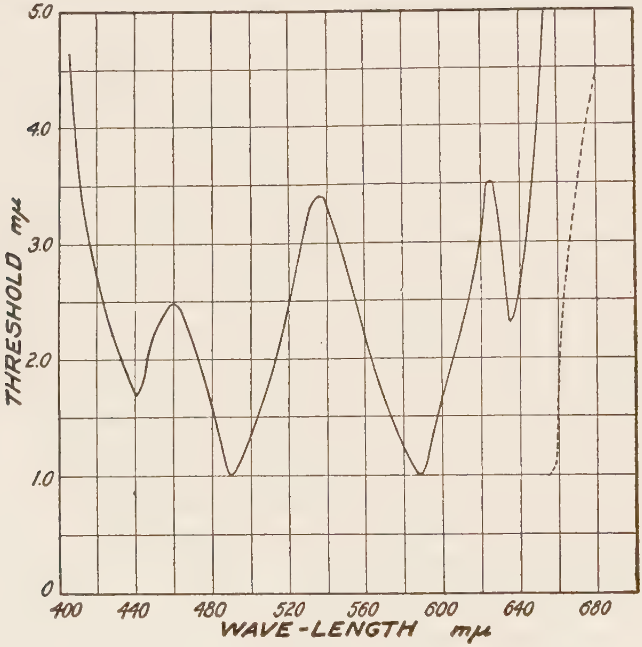


FIG. 53. WAVE-LENGTH DISCRIMINATION AS A FUNCTION OF WAVE-LENGTH.

This curve represents the changes in slope of the curve in Fig. 52, and shows how the just-noticeable difference in wave-length varies over the spectrum. The dotted portion of the curve is plotted on a scale five times that of the main portion, indicating the extreme depression of wave-length sensibility in the red.

TABLE VII

The Spectral Chroma Scale

No.	λ(*mμ*)	*d*λ	No.	λ	*d*λ	No.	λ	*d*λ
1	700.0	....	44	576.5	1.4	87	490.4	1.1
2	678.0	22.0	45	75.2	1.3	88	89.4	1.0
3	65.0	13.0	46	73.7	1.5	89	88.2	1.2
4	59.0	6.0	47	71.7	2.0	90	87.0	1.2
5	54.0	5.0	48	70.1	1.8	91	85.8	1.2
6	49.5	4.5	49	68.4	1.7	92	84.5	1.3
7	46.0	3.5	50	66.6	1.8	93	83.2	1.3
8	42.8	3.2	51	64.8	1.8	94	81.7	1.5
9	40.2	2.6	52	63.0	1.8	95	80.0	1.7
10	37.8	2.4	53	61.1	1.9	96	78.2	1.8
11	35.5	2.3	54	58.6	2.5	97	76.5	1.7
12	33.1	2.4	55	57.0	2.6	98	75.0	1.5
13	30.0	3.1	56	54.4	2.6	99	72.9	2.1
14	26.5	3.5	57	51.8	1.6	100	70.5	2.4
15	23.0	3.5	58	49.1	2.7	101	68.2	2.3
16	20.0	3.0	59	46.1	3.0	102	65.8	2.4
17	17.3	2.7	60	43.0	3.1	103	63.6	2.2
18	14.9	2.4	61	39.8	3.2	104	61.2	2.4
19	12.5	2.4	62	36.5	3.4	105	58.7	2.5
20	10.2	2.3	63	33.2	3.3	106	56.5	2.2
21	08.0	2.2	64	30.1	3.1	107	54.4	2.3
22	06.0	2.0	65	27.1	3.0	108	52.1	2.3
23	04.1	1.9	66	24.2	2.9	109	50.0	2.1
24	02.3	1.8	67	21.4	2.8	110	48.0	2.0
25	600.6	1.6	68	19.1	2.3	111	46.0	2.0
26	599.0	1.6	69	16.8	2.3	112	44.2	1.8
27	97.4	1.6	70	14.6	2.2	113	42.5	1.7
28	95.9	1.5	71	12.6	2.0	114	40.8	1.7
29	94.5	1.4	72	10.6	2.0	115	39.0	1.8
30	93.1	1.4	73	08.0	1.6	116	37.2	1.8
31	91.8	1.3	74	07.0	1.0	117	35.3	1.9
32	90.5	1.3	75	05.4	1.6	118	33.3	2.0
33	89.5	1.0	76	04.0	1.4	119	31.3	2.0
34	88.5	1.0	77	02.6	1.4	120	29.3	2.1
35	87.5	1.0	78	01.3	1.3	121	27.0	2.2
36	86.4	1.1	79	500.0	1.3	122	24.8	3.2
37	85.3	1.1	80	498.7	1.3	123	22.3	2.3
38	84.0	1.3	81	97.4	1.3	124	19.7	2.8
39	82.7	1.3	82	96.1	1.3	125	16.7	3.0
40	81.5	1.2	83	94.8	1.3	126	13.8	2.9
41	80.3	1.2	84	93.7	1.1	127	10.4	3.4
42	79.1	1.2	85	92.6	1.1	128	405.8	4.6
43	77.9	1.2	86	91.5	1.1	....	....	......

The appearance of the spectrum to color-blind individuals departs radically from the above description. In the most common form of partial color-blindness, the dichromatic type, the color spectrum is divided into two distinct ranges, that corresponding to the longer waves being yellow, while the opposite end-region is blue. Between these two zones, there is a very narrow gray band, the exact position of which differs somewhat with the kind and degree of the color-blindness. The laws connecting wave-length discrimination with wave-length, for dichromatic vision, take the form shown in Fig. 54. They are evidently simpler than for normal trichromatic vision, confirming the notion that the dichromatic form is a reduction system produced by the

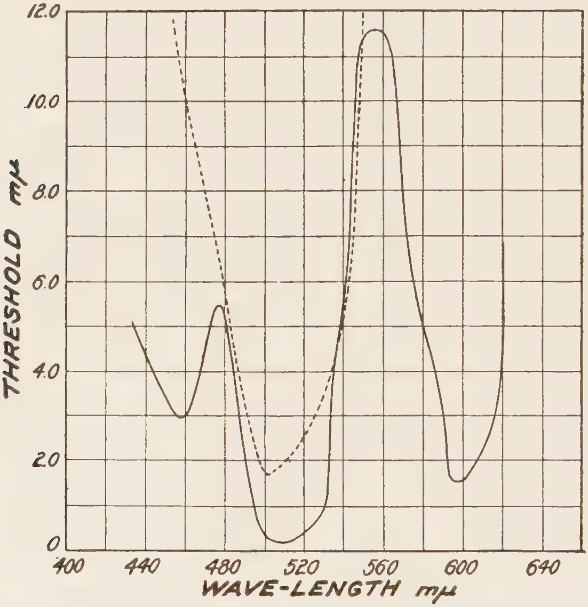


Fig. 54. Wave-length Discrimination for Dichromatics.

The two curves in this figure correspond in general principle with the single curve of Fig. 53, but are for partially color-blind subjects. The dotted curve represents the wave-length discrimination of the deuteranopic type while the solid line represents that for the protanopic type.

dropping out of some component which is present in trichromatic vision. It is impossible here to enter into detail regarding these relations for all types of color-blindness, and, indeed, adequate data are, in general, absent.

No careful studies have thus far been made concerning the dependency of the spectral chroma scale upon intensity, but facts which we shall consider later indicate that the laws depicted in Figs. 52 and 53 can hold only over a mid-range of intensities, although the region is probably quite broad.

304. The Purples. — The failure of the purple hues to appear in the spectral series shows that they require a complex stimulus. If we define the purples as blue-reds or red-blues, the violet must be classed with them. On the other hand, if we regard them as chromas which are produced by mixtures of long and short wave stimuli, then the psychologically primary red is a purple. The choice of stimuli for the production of purples is fairly flexible, but for maximal saturation their wave-lengths must be greater than about 660 $m\mu$ and less than about 478 $m\mu$, respectively. F. O. Smith[453] has determined the number of just noticeable steps from blue-violet to red, through the purple series, using broad-banded (filter) stimuli, and finds the number to be 28, at a fairly low intensity. His experimental procedure involved changes in brilliance, as well as in hue, and the total number of steps was found to decrease, with decreasing absolute intensity. However, in combination with Jones' data, the indications are that the total cycle of maximally saturated hues comprises less than 156 just noticeably different members. A study of the number of hue steps in a cycle of chromas which are all of the same saturation is greatly to be desired.

305. Saturation as a Function of Wave-Length. — Even a cursory examination of the spectral chromas shows that they are not of equal saturation. It is introspectively evident that the spectral yellow resembles white more than do the red or the blue. Jones and Lowry[454] have recently made a systematic determination of the saturations of eight representative spectral colors. They stepped off the distance from white to the spectral chromas in just noticeable differences, using homogeneous stimuli mixed with radiation having the distribution curve of a "black body" at 5200° K. The number of steps found were as follows:

TABLE VIII

Saturation Scale Data

Wave-Length	440	470	490	540	575	605	640	680
No. of Steps	23	22	19	19	16	20	23	23

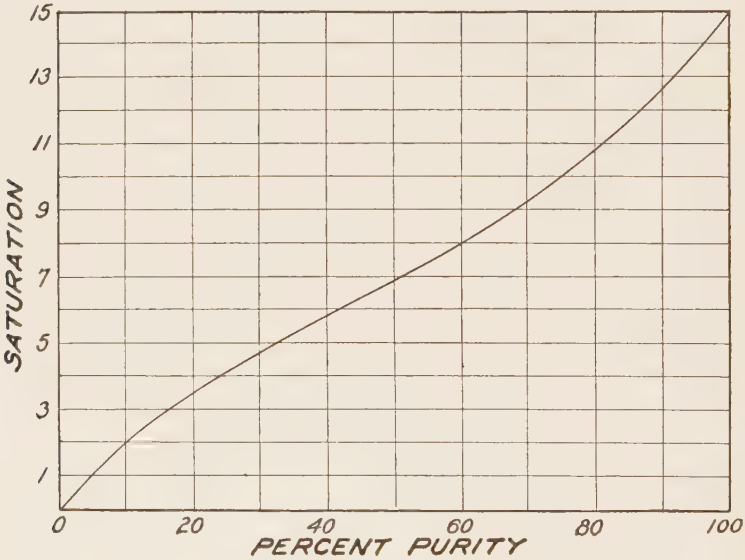


Fig. 55. The Dependency of Saturation Upon Stimulus Purity.

This curve, reconstructed from the work of Jones and Lowry, shows how saturation increases as the ratio of spectral stimulus to "white" is increased in a mixture. The curve is an average for all spectral stimuli, but the ordinates are proportional to saturation scale number and yield absolute saturation readings for a color whose maximal saturation is 15.

It will be seen that the yellow shows a minimum, as expected, while the violet and red are equal in saturation. If we define purity as the proportion of homogeneous to heterogeneous *light* in the stimulus mixture, we can plot the relationship between this variable and saturation scale position, as in Fig. 55. The data for the eight wave-lengths are reduced to an arbitrary maximum of fifteen steps, in order to demonstrate the similarity between the several individual curves. It will be seen that the sensibility to change in purity shows maxima at zero and 100 percent.

Evidence regarding the relative saturations of the spectral chromas also appears in other relationships. The facts of color mixture, to be considered in detail below, indicate a variation in inherent saturation generally similar to that demonstrated by the data of Jones and Lowry. The rate at which flicker ceases when a chromatic stimulus is alternated with " white " in the flicker photometer also varies in a similar manner over the spectrum. It is to be anticipated that this " flicker photometer frequency " will be greater, the greater the difference between the given chroma and the white. I have found[455] that the amount of white which must be mixed with spectral stimuli to yield equal flicker photometer frequencies, conforms to a function similar to that demanded by Jones and Lowry's results.

Another index of saturation is to be found in what may be called the *relative chromatic threshold,* or the amount of chromatic stimulus which must be added to a " white " stimulus of fixed intensity in order to yield a just-noticeably chromatic color. Purdy, working in my laboratory, has determined this threshold as a function of both the wave-length of spectral stimuli and the intensity of the " white." In terms of photons, he finds the threshold to show a definite maximum in the spectrum at 575 $m\mu$, falling off rather more sharply on the long-wave than on the short-wave side. However, if one plots the ratio of " white " to spectral intensity (both in photons), the curve becomes practically identical with that of Fig. 62, indicating that this ratio, as might be expected, is proportional to the chroma-brilliance coefficient of the given spectral stimulus. However, Purdy's results show that the proportionality constant increases progressively with the intensity of the " white " or of the total mixture.

II. CHROMA AS A FUNCTION OF WAVE-LENGTH COMPOSITION

When the stimulus which evokes a color is not spectrally pure, but consists of a mixture of rays having different wave-lengths, the dependencies of hue and saturation upon its composition become very complex. However, these relationships have been studied very diligently, so that we are able to formulate them in a very accurate and comprehensive manner. Since an infinite number of wave-length combinations are possible, it is necessary to restrict the discussion to certain typical cases, although laws can be presented which apply to all possible combinations. We shall consider, first, the chromas evoked by mixtures of two homogeneous wave-lengths and then of three such wave-lengths variously located in the spectrum. It will appear that mixtures of more than three wave-lengths can be interpreted in terms of the result obtained with a three-component stimulus when the components are properly chosen. It will be most convenient to consider the variations in hue and in saturation together.

306. The Psychophysics of Two-Component Mixtures.— *With One Extreme Long-Wave Component.* — Let us choose a substantially homogeneous stimulus, having a wave-length of 760 *mμ,* which corresponds very closely to the limit of visibility at the long-wave end of the spectrum. Let us consider a second homogeneous ray, of variable wave-length, to be mixed with the stimulus thus selected. If the former lies anywhere between 760 *mμ* and 660 *mμ*, the hue and saturation of the mixture will be indistinguishable from those which are evoked by either of the two stimuli taken alone. This is to be expected from the fact that, within the given range, the chromatic values of homogeneous stimuli are substantially invariable. When the variable component in the mixture has a wave-length smaller than approximately 660 *mμ,* the hue evoked by the mixture will be one which is intermediate in the hue cycle between that characteristic of wave-length 660 *mμ* and that which normally accompanies stimulation with the given variable wave-length, provided the latter is not less than about 490 *mμ.* If the variable wave-length is not reduced below approximately 590 *mμ,* the saturation of the mixture will be equal to that of a spectral color matching the mixture in hue. In other words, between the extreme long-wave end and about 590 *mμ,* there is a region from which mixtures may be selected capable of matching spectral colors both in hue and saturation.

Complementaries. — When the wave-length of the variable component is made smaller than about 590 *mμ,* the saturation decreases as the wave-length is reduced, becoming zero at about 490 *mμ,* the wave-length already specified, provided that a certain ratio of intensities between the two components is employed. If the intensity ratio differs from the required value, the mixture will exhibit a hue identical with the hue of the component which predominates in intensity, and the saturation will increase as such predominance increases. The wave-lengths of stimuli which can be mixed in some proportion to evoke a color of zero saturation, *i.e.,* a gray, are called *complementary wave-lengths;* and the chromas which accompany excitation with such stimuli, taken individually, may be called *complementary chromas.* It should be borne in mind that the complementary stimuli produce " white " or " gray " only when mixed in a single definite ratio of intensities, although their mixtures are characterized, at all intensity ratios, by relatively high desaturation and the absence of hues other than those individually characteristic of the components.

With One Extreme Short-Wave Component. — Let us now consider, analogously with the above discussion, what happens when the fixed component of a two-element mixture is chosen at the extreme short-wave end of the visible spectrum, say at 430 *mμ,* while the variable component has a longer wave-length. We find in this case a comparatively short region, only a few *mμ,* in which the hue of the mixture is identical with that of the component, although a larger, but still relatively small, interval in which the saturation is thus equivalent. This constant saturation band extends from 430 $m\mu$ to about 470 $m\mu$. If the wave-length of the variable component is taken greater than 470 $m\mu$, the saturation decreases as the wave-length in question increases, becoming zero, with a proper intensity ratio, at about 570 $m\mu$. The latter is the complementary of the extreme short-wave stimuli, just as 490 $m\mu$ is that of the extreme long-wave rays. With wave-lengths of the variable component less than 570 $m\mu$, the hue of the mixture is that of a chroma on the color solid intermediate between those which are characteristic of the two components taken individually, the exact hue depending upon the intensity ratio of those components. The law governing this dependency of the hue of a mixture upon the relative intensities of the two mixture stimuli will be considered below.

Other Cases of Two-Component Mixture.—A third typical two-component mixture consists of the two extreme spectral wave-lengths taken together. We have already seen that the colors, evoked by such a mixture, possess hues which lie on the color cycle intermediate between the slightly orange-red and the violet, and known as purples. Their saturations have not been studied carefully, but seemingly differ very little from those of the components, regardless of the intensity ratio in which the latter are applied. The exact position of the resultant purple hue, however, depends upon this ratio, as in the case of other mixtures.

When we experiment with mixtures which are not based upon fixed components at the spectral extremities, we find that their hues and saturations follow laws similar to those applying to the three typical cases above considered. The hue is intermediate on the short segment of the color cycle determined by the two components, and the saturation is decreased, as compared with the saturations of the components taken alone, unless both components lie within the two zones already indicated as lying at either end of the spectrum. The degree of relative desaturation is greater, the nearer the two components in the mixture are to being complementaries, and also the closer the ratio of their intensities to that which is required of complementary stimuli to evoke a true neutral gray. As the longer wave component of a two-element mixture is removed from the extreme long-wave end of the spectrum, the wave-length of the other component required to yield a gray also becomes shorter until the extreme short-wave end of the spectrum is reached. Under these conditions, the first mentioned component must itself be the complementary of the extreme short-wave stimulus.

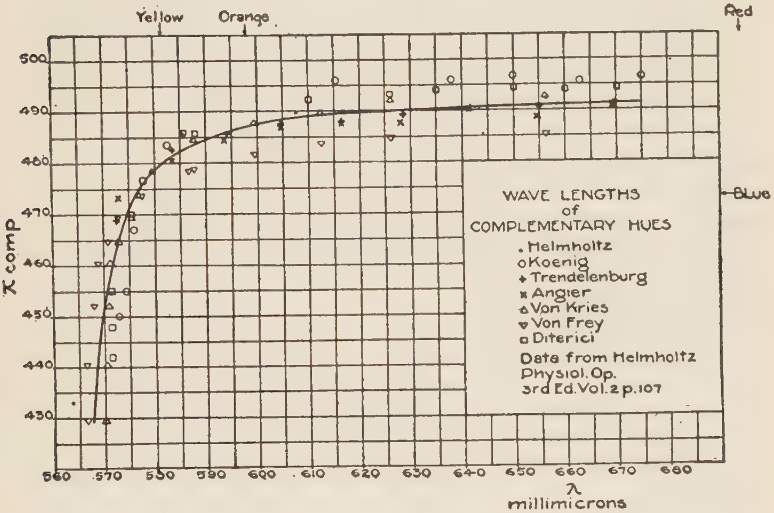


Fig. 56. Wave-lengths of Complementary Spectral Stimuli.

This curve, due to Priest, summarizes the data of a number of independent investigators, as shown.

Exactly parallel reasoning applies to mixtures based upon progressively increasing wave-lengths, starting at the short-wave end and ending at the wave-length which is complementary to the extreme long-wave rays. Thus it follows from the locations of these two limiting complementaries at 570 *mμ* and 490 *mμ,* respectively, that there is a spectral region, *viz.,* the one between the two specified wave-lengths, for all wave-lengths within which there exist no homogeneous complementaries. The chromas evoked by stimuli lying within this region all possess a greenish tinge, so that the facts may be expressed roughly by saying that greens have no spectral complementaries. It is a common observation, of course, that the complementary of green is purple, but it will immediately be realized that the latter rests upon a heterogeneous stimulus consisting of the two spectral extremes taken together.

307. The System of Spectral Complementaries. — For each wave-length in a restricted end-region of the spectrum, a complementary wave-length can be found in the other end-region. The results of determinations of these pairs of wave-lengths by Helmholtz and others have been combined by Priest [456] to yield the curve shown in Fig. 56. Priest finds that the relation between the complementary stimuli corresponds very closely to a rectangular hyperbola, having the equation

$$(530 - f)(f_c - 608) = 220,$$

where f is a stimulus frequency and f_c is that of its complementary. The frequency is expressed in terms of the number of vibrations per one-trillionth of a second. The relationship is also hyperbolic with respect to wave-length, although the fit of the data is not quite as satisfactory. Sinden [457] has recently made a very careful determination of the spectral complementaries, upon his own eye, with the following results:

TABLE IX

WAVE-LENGTHS OF SPECTRAL COMPLEMENTARIES

Given Wave-Length	*Complementary Wave-Length*	*Ditto Nine Observers*
Extreme red	496.5	497.1
609	493.5	
609.5		494.1
591	490	
586	487.5	
581		485.5
580	482.5	
578.5	480.5	
576.5	477.5	
575.5	474.5	
574	472	
573	466.5	
572	459	
570.4		Violet
570	Extreme violet	

The figures in the third column are the averages for nine different observers. Sinden used the spectral distribution of average noon-sunlight at Washington as a standard "white." Further results of his studies will be discussed below. (*Cf.* pages 166–167 and 185.)

308. The Psychophysics of Three-Component Mixtures. — The above analysis of the results obtainable with two-component mixtures makes it evident that, when the wave-lengths of the components are properly chosen, a fairly wide range of chromas can be evoked by varying the ratio of the two intensities. The same analysis indicates that, if *three* suitably selected constituents are employed, a very much larger number of colors can be evoked by a variation of relative intensities alone, while all wave-lengths remain fixed. Suppose, for example, that the three components which we choose are the extreme long-wave and the extreme short-wave visible stimuli, together with a stimulus whose wave-length lies halfway between the complementaries of the two extreme-wave stimuli, *viz.*, at about 530 $m\mu$. Then, by mixing the last-mentioned ray with the longer wave component, in various proportions, we can evoke all hues intermediate between the two components. A similar statement holds for varying mixtures of the 530 $m\mu$ stimulus with the shorter wave constituent. The two extreme spectral members, taken together, permit the production of a complete purple scale, so that by means of these three stimuli, used in pairs, the entire hue cycle can be traversed. Using them "in pairs" means simply that the intensity of one of the three has been reduced to zero.

When all three elements have a finite value, the colors of the resulting mixtures will be less saturated than when the elements are taken "in pairs," and this relative desaturation may be of any amount, since a proportion of the three can be found which will yield a completely neutral gray. Thus, by means of three components fixed in wave-length but variable in relative intensity, we can evoke all of the colors lying in a section through the psychological color solid, at any desired brilliance level. This is the psychophysical basis of the so-called *principle of three-color mixture* or analysis, a principle which, in practice, permits a nearly perfect reproduction of all common colors, by varying the proportions of three constituents having fixed wave-length constitutions.

However, it is not possible to make a selection of three stimuli, thus fixed as to wave-length, by means of which the *spectral* colors can be matched in saturation. Indeed, except within the zones of equivalent saturation already described above, there is no selection of any number of components which will yield a perfect saturation match with the spectral color of the same hue, although in limiting cases the discrepancy can of course be reduced below the threshold. The most feasible method of dealing with mixtures containing a plurality of components greater than two, is to determine the hue and saturation resulting from a given pair of components, and then to consider this color as a member in a new pair containing also a further component, repeating this process until all of the constituents have been considered. The most convenient scheme for carrying this out quantitatively involves the so-called color-mixture triangle, which is based upon the empirical reproduction of a representative variety of colors by the mixture of three components, but which has been extended theoretically so as to cover all possible cases.

309. The Color-Mixture Triangle. — The color-mixture triangle should not be confused with the psychological color solid (see Note A), although it bears some resemblance to a section of the latter, taken perpendicularly to the achromatic axis. The color solid is a purely psychological or introspective construction, whereas the color-mixture triangle is psychophysical in its significance. The units employed in the two schemes are utterly different, those of the solid being just noticeable differences, whereas those of the triangle are defined in terms of color-mixture results and depend, at least in part, upon physical measurements.

A color-mixture triangle can be constructed by employing three elementary stimuli, properly chosen, in the following general manner. These stimuli need not be individually homogeneous, but it is assumed for simplicity of argument that they can be combined in ratios of positive values to evoke a gray, although it is mathematically possible to utilize negative values. The first step is to determine the intensities which yield the gray, after which these intensity values are taken as equal, and as units in terms of which all other values may be expressed. The equality, thus defined, is one of *chromatic valence,* a quantity which, for different wave-length compositions, is in no way proportional to either photometric or radiometric intensity, although such a proportionality can be established for any fixed wave-lengths.

Having specified the units in this manner, we may proceed to represent all possible combinations of the three components by means of points in an ordinary three-dimensional plot, employing Cartesian coördinates. Such a representation, however, involves variations in the total intensity of the mixture, not merely in the proportion of the three combined intensities, and it is this *proportion,* only, which is of interest in considering the chromatic attributes. In order to abstract from the total intensity, or the brilliance dimension, we may confine our attention to a section of the coördinate system, which is enclosed within the three reference planes and perpendicular to the axis of the solid angle thus defined. Such a section, as shown in Fig. 57, is triangular in outline, and comprises a color-mixture triangle of the type which we are considering. Points within the triangle obviously represent ratios, rather than absolute values. In the original Cartesian diagram, the absolute intensities were measured perpendicularly to the reference planes, so that, in the triangle, the ratio measures must be represented by means of lines drawn from any point perpendicularly to each of the three sides. The lengths of these lines, as determined by the given point and the intersection with the respective sides, must be in the same ratio as the chromatic valences in the mixture.

A careful study of this somewhat unique system will show that its geometrical characteristics imply the following propositions: When any two elements, represented by two points in the triangular surface, are mixed in a given intensity ratio, the resulting color is represented by a point lying on the straight line connecting the two points in question. Moreover, if the relative intensities are considered as masses operating at their respective extremities of the line, the location of the resultant will be at the "center of grav-

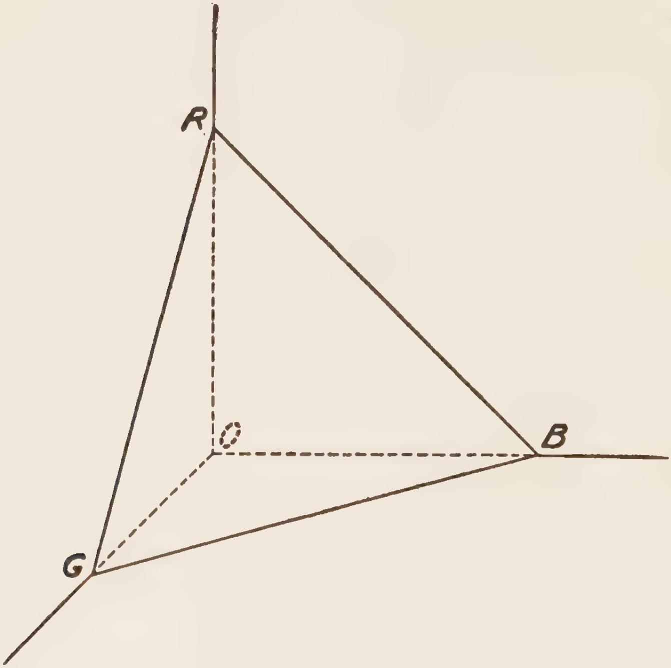


Fig. 57. The Color-mixture Triangle in Relation to Tri-dimensional Coördinates.

This diagram shows how the trilinear system of coördinates which is used in the color-mixture triangle is related to a system of ordinary three-dimensional Cartesian Coördinates. Absolute values of three independent variables, plotted with respect to the latter, find relative representation when the points standing for them are projected upon the triangular surface in the direction of the origin, *O*.

ity" of the line. This "centroid" principle holds for any number of components, however they may be scattered over the plane of the triangle, since we may find the center of gravity for any two of them and then combine the result with a further element in the same manner, and so on. Consequently, the triangle provides us with a means for determining the chromatic value of the color given by any mixture of components, no matter how complex, provided only that we are able to specify the positions of all of these components in the triangle. A particularly important case, involving the combination of three elements, is that of the three primaries upon which the triangle is based. These primaries are located at the three corners of the triangle, and their equal mixture must lie at the center of gravity of the triangle as a whole, representing "white."

The stimuli which correspond to the primaries in question may be standardized in any desired manner and may be chosen in a wide variety of ways, although it is most convenient to select spectrally homogeneous primaries. In any case, the locus of the spectral colors, within the plane of the triangle, is of peculiar interest. However, even when the primaries are themselves homogeneous, the spectral locus lies in general outside of the triangular area. This is to be expected from the fact that mixture usually produces desaturation. The most easily understandable experimental procedure for determining the spectral locus with respect to the triangle is to employ a two-part photometric comparison field, on one half of which is presented a variable mixture of the three selected primary stimuli, while on the other half any desired single spectral stimulus may be combined with a "white." We can then match the spectral color in hue by varying the proportions of the three primaries, while the two saturations can be balanced by altering the ratio of the spectral stimulus to the neutral one.

The results of such a procedure, for the entire range of the spectrum, are shown in the three curves of Fig. 58, which is replotted from the recent measurements of Wright[458] upon ten subjects. The primary spectral stimuli in his experiments had wave-lengths of 460, 530, and 650 *mμ*, respectively, and the curves represent the relative amounts of these primaries required to yield matches at each wave-length, using units such that equal amounts of the three give white or gray. In order that the data should be expressed in terms of the primaries alone, the saturation losses are indicated by *negative* values. Such negative quantities correspond to amounts of the primaries which must be added to the spectral color that is being matched, in order to give an equation of saturation as well as of hue. The effect of such an addition, in the given instances, is to produce the required amount of white through complementary action.

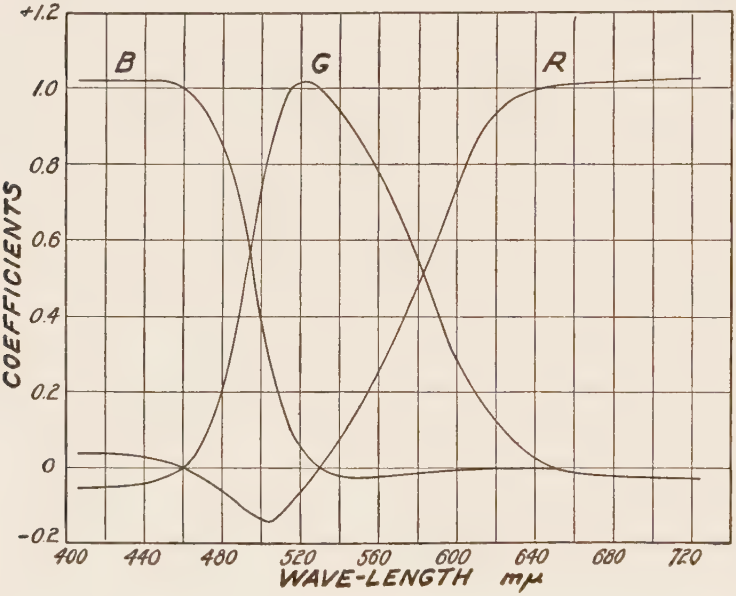


FIG. 58. THREE-COLOR MIXTURE RATIOS TO MATCH SPECTRAL HUES.

The three curves in the figure represent the average results of Wright upon ten subjects. The wave-lengths of the primary stimuli were: B, 460 *mμ*; G, 530 *mμ*; and R, 650 *mμ*. Where the values are negative, the given primary had to be added to the spectral color, which was being matched, in order to secure an equation of saturation as well as of hue.

When data of this sort are plotted with respect to the trilinear coördinates of the color-mixture triangle, the result is a diagram of the type shown in Fig. 59. In this case, however, the data are those of Ives and of König, involving primaries of wave-lengths 436, 520, and 656 $m\mu$. In attempting to develop a theoretical conception of the mechanism underlying chromatic vision, it may be desirable to regard the spectral colors as being determined by ratios of excitation values, all of which are positive. This demands a reconstruction of the triangle, in terms of ideal elementaries some of which — particularly, the green — have saturations greater than the corresponding spectral primaries. It may also be useful to employ primaries having non-spectral (or purplish) hues. The required transformation can be carried out by means of the general mathematical properties of the triangle, as already explained above. One of the

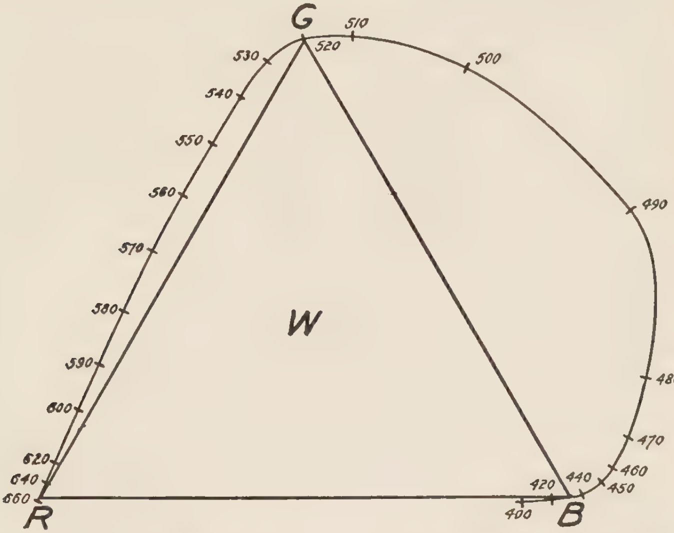


Fig. 59. Color-mixture Triangle with Spectral Locus Outside.

This figure shows how the negative values of Fig. 58 cause the locus of the spectral colors to lie outside of the corresponding color-mixture triangle. The data are those of Ives, rather than of Wright, involving slightly different primaries.

most interesting of such reconstructions is shown in Fig. 60. It is due to Ives,[459] but involves a method of choosing the primaries, first suggested by König, such that the two types of dichromatic vision (protanopia and deuteranopia — see page 164, below) can be explained by a dropping out of either the red or the green curve, respectively. The red primary in this system is more bluish than the extreme spectral red, while the green is more than spectrally saturated.

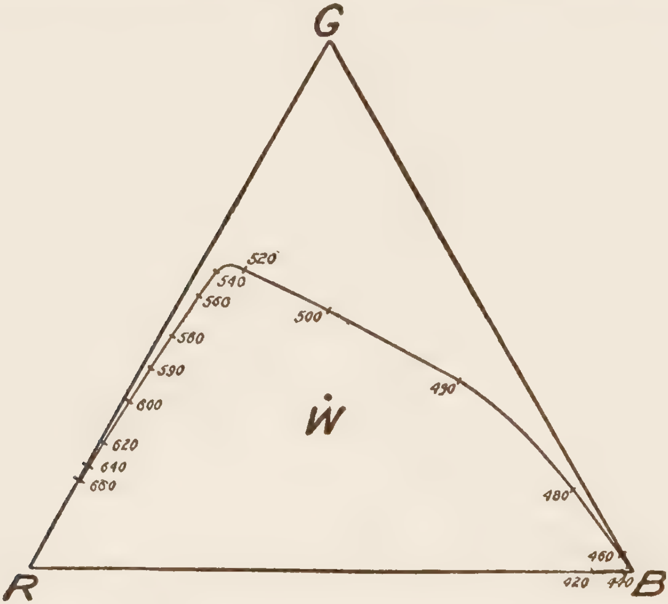


FIG. 60. RECONSTRUCTED COLOR-MIXTURE TRIANGLE.

In this figure, the color-mixture triangle has been reconstructed in accordance with principles explained in the text, so that the spectral locus will fall inside of the triangle, and so that the primaries will be suitable for the explanation of certain facts of color-blindness.

The curves of Fig. 58, being indicative of mixture ratios only, do not represent the variations in brilliance or visibility in the spectrum. However, three variables are sufficient to specify both the chromatic and achromatic features of the system, if the primaries are evaluated in terms which are proportional to their visibility or light values. Fig. 61 shows the outcome of such an evaluation of Wright's data. Table X presents the combined results of König and of Abney in similar form, but modified so that the three curves enclose equal areas, under which condition they are described as "excitations."

TABLE X

Spectral Colors in Terms of Elementary Excitations

Wave-Length mμ	*Excitations*			*Percentages*		*Wave-Length*	*Excitations*			*Percentages*	
	Red	*Green*	*Violet*	*Red*	*Violet*		*Red*	*Green*	*Vio-let*	*Red*	*Vio-let*
400	...	...	253	...	100	550	424	612	18	40.2	1.7
410	...	...	433	...	100	560	466	578	11	44.2	1.0
420	...	...	614	...	100	570	505	517	7	49.5	.7
430	...	...	915	...	100	580	520	415	4	55.4	.4
440	...	7	1019	...	99.3	590	535	296	..	64.3	..
450	...	16	950	...	98.3	600	510	196	..	72.2	..
460	...	38	842	...	95.7	610	462	113	..	80.4	..
470	...	81	697	...	89.6	620	375	59	..	86.3	..
480	14	122	473	2.3	77.6	630	285	29	..	90.8	..
490	41	169	220	9.5	51.1	640	195	10	..	95.1	..
500	83	260	123	17.8	26.4	650	118	3	..	97.5	..
510	151	391	87	24.0	13.8	660	68	...	..	100	..
520	233	510	61	29.0	7.6	670	40	...	..	100	..
530	307	572	43	33.3	4.7	680	22	...	..	100	..
540	373	603	29	37.1	2.9	690–750	27	...	..	100	..

It will be noted that, in all of the color-mixture triangles, the mid region of the spectral locus runs much closer to the point representing gray or white than do its extremities. This shows that, in terms of chromatic valence, the mid-spectral colors are less saturated than are those lying at the spectral extremities, a result which harmonizes with observations upon spectral saturation made by other methods, as already discussed.

310. Abnormal Color-Mixture Relations. — The general principles of color-mixture, above outlined, apply to abnormal (color-blind) individuals as well as to the normal. However, the exact position of the spectral locus varies with the type of abnormality, being different, for example, for the so-called anomalous trichromatics[460] as compared with the normal trichromatics. Moreover, for both forms of dichromatic vision, the results of color-mixture can be expressed on a two-dimensional diagram or a single straight line, a surface not being required, so that the triangle may be regarded as being reduced in these cases to the equivalent of one of its boundaries. For the green-blind, or deuteroanopes,[460] this is approximately the red-blue boundary of Fig. 60, while for the red-blind, or protanopes, it corresponds to the green to blue line.

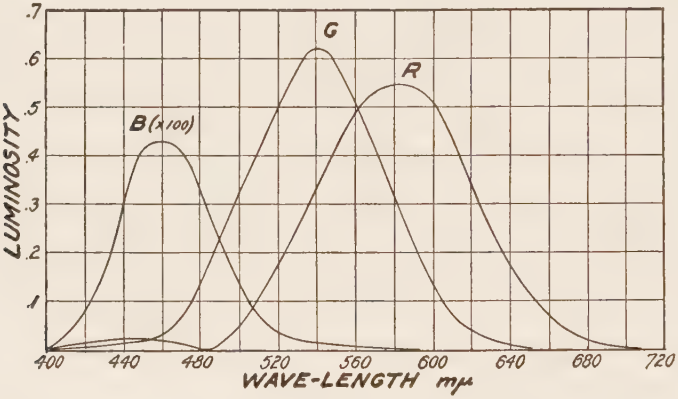


Fig. 61. Color-mixture Curves in Terms of Luminosity Values.

The three curves in this figure represent the results of Wright, replotted in terms of light values, rather than as ratios, required to match the spectral colors. On account of extremely low luminosity value of the short-wave *B* primary its ordinates have been multiplied by a factor of 100.

In each case the spectral locus lies upon the boundary in question, and all of the spectral colors can be matched by mixtures of two properly selected spectral components. Moreover, since all possible colors can be represented on a single line, any color can be matched by a single properly chosen spectral color, one of the latter, as already noted, being in fact a match for the color evoked by "white" or gray light. A further conceivable form of dichromatic vision, which, however, seems to be quite rare in reality, would be represented by the red to green boundary of the normal color triangle. Other forms are possible and known, corresponding to lines drawn within the triangle between definite points. Monochromatic vision, or "total color-blindness," has no color-mixture characteristics. All mixtures are represented by the same point in the triangle, presumably that corresponding to "white."

311. Brilliance Relations of the Color-Mixture System. — The principles of color-mixture which have been presented above, have been expressed uniformly in terms of what is known as chromatic valence, based upon the assumption of equality between stimuli which yield a gray, when mixed. Although this may seem to be an arbitrary basis of measurement, it is more useful for the given purpose than one involving photometric or energy equations. We have already seen that energy units are awkward, even in formulating visual relationships which involve brilliance; and a similar situation obtains with respect to photometric units, when dealing with the phenomena of color-mixture. This is due to the great disproportionality which exists between the chromatic and the achromatic (brilliance) values of the stimuli. The discrepancy in question is so great between the violet and its complementary, greenish yellow, that the quantity of the former, required to neutralize the latter chromatically, yields an almost inappreciable increase in the brilliance or photometric value.

Now, it is possible to construct a color-mixture triangle in which the dimensions are determined by photometric measurements, but its form is so elongate in one direction as to render it of little practical value. However, if we know the factors which relate the photometric values of the three elementary stimuli to their chromatic valences, we can compute the position of any mixture or color in such a triangle. Each color evidently possesses a characteristic factor of this sort, which may be designated as its chroma-brilliance coefficient, representing the chromatic valence per unit of photometric intensity. These coefficients are high at the short-wave end of the spectrum and low at the long-wave end. Abney [461] found that the red, green, and blue of his color-mixture system had photometric values of 450, 192, and 2.53, respectively, when chosen so as to yield a white by mixture. The chroma-brilliance coefficients would vary inversely as these values. Such coefficients are of particular interest for the case of complementary spectral stimuli which, when mixed in such proportions as to yield a gray, must have equal chromatic valences. The photometric values required of typical pairs of complementaries, as found

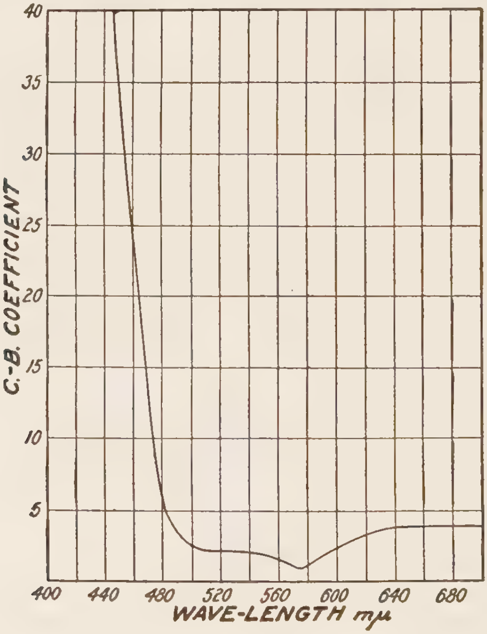


Fig. 62. Relative Luminosities of Spectral Complementaries.

The ordinates of this figure represent the reciprocal of the light value, required at the given wave-length, to match a "white" of fixed light value, by mixture with the complementary wave-length. The curve is copied from the work of Sinden. See text for discussion.

by Sinden, enabled him to estimate the coefficients for the entire range of spectral colors, as shown in Fig. 62.

III. CHROMA AS A FUNCTION OF INTENSITY

312. Saturation and Intensity. — Both hue and saturation vary, in an important manner, as functions of the stimulus intensity. The exact modes of variation differ rather radically with the position of the stimulus in the visual field and with the state of adaptation. Since scotopic response is achromatic and occurs at low levels of intensity where photopic response is impossible, we must find that saturation decreases at very low intensities and chromas tend to be replaced by grays, regardless of the wavelength composition of the stimulus. However, since the extreme long-wave (red) rays do not arouse the scotopic mechanism, they may — and do — constitute an exception to this principle. The low-intensity saturation losses with other rays will naturally be greater in the periphery than in the center of the visual field, and will be favored by scotopic dark adaptation.

The Photochromatic Interval. The intensity range between the absolute brilliance threshold and the point at which chroma is first distinctly evoked is called the photochromatic interval.[462] For wave-lengths greater than about 665 $m\mu$, this interval is zero in all parts of the visual field, except possibly in the extreme periphery, where chromatic response tends to be absent in general. One might expect it to be absent for all wave-lengths in the center of the field, in correspondence with the absence of scotopic response (and retinal rods) at this position. The recent investigations of D. McL. Purdy, in my laboratory, however, leave no doubt as to its presence. The values of the interval, as found by Purdy for spectral stimuli, are shown in Fig. 63. The fact that the interval becomes zero at a wave-length coinciding with long-wave end of the scotopic visibility curve suggests that the foveal effect may be referable to a residual amount of scotopic vision. However, Purdy finds that the interval is increased, rather than being reduced, by diminishing the size of the central area which is stimulated, a result which is inconsistent with the general law of distribution of scotopic response over the visual field.

Intensity Conditions for Maximal Saturation. When the intensity of the stimulus is raised above the absolute chromatic threshold, the saturation increases to a maximum and then, with still further intensity augmentation, it decreases again. Using a direct introspective criterion of saturation, Purdy has determined the intensities at which maximal saturation is evoked by the various wave-lengths of the spectrum. His results are given in Table XI. It will be noted that the optimal intensity for saturation is smallest at the short-wave end of the spectrum, mounting steadily, with decreasing wave-length, to a maximum at about 565 $m\mu$ and then falling suddenly to a value which is practically independent of wave-length between 600 and 700 $m\mu$. Comparison of these results with the various indices of the

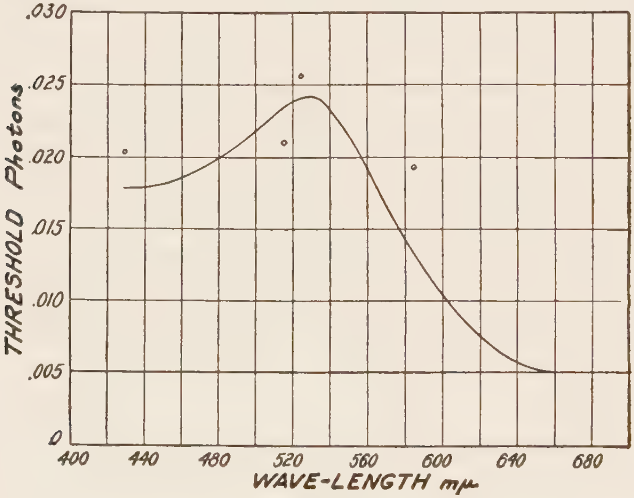


Fig. 63. Distribution of the Foveal Photochromatic Interval in the Spectrum.

Assuming the absolute brilliance threshold to be constant at 0.005 photons, this curve shows the values of the absolute chromatic threshold relative to the brilliance threshold. The curve is plotted from the data of Purdy. Determinations which do not fall satisfactorily on the curve are shown by circles.

manner in which saturation varies as a function of wave-length points to the following law: *The more saturated a hue is, the lower is the intensity at which its saturation finds a maximum.* It is generally conceded that for intensities beyond the position of the maximum, saturation decreases constantly so as to become zero at extremely high values of the stimulus.

TABLE XI

INTENSITY REQUIRED FOR MAXIMAL SATURATION

Wave-Length *mμ*	*Intensity* *Photons*
700	42
440	9
460	12
470	15
480	24
490	19
505	62
515	85
525	155
540	193
550	181
555	182
565	219
575	175
585	134
592	64
600	49
620	57
635	376
660	44
700	42

313. Hue and Intensity. — *The Bezold-Brucke Effect.* The changes in saturation, which occur as the stimulus intensity is increased, are accompanied by equally important shifts in hue. Four hues in the color cycle, corresponding at least approximately to the psychological primaries, remain invariable, except as to saturation. The hues evoked by other stimuli alter in the manner indicated by the arrows and plot in Fig. 64. The psychological blue and yellow behave as if they represented points of stable equilibrium in the chromatic system, while the primary red and green simulate a condition of unstable equilibrium. The reddish and greenish hues shrink away from their prototypes towards the yellow or blue, in accordance with their initial locations in the color cycle.

When homogeneous or spectral stimuli are employed, the shifts in hue between given pairs of intensities follow a law similar to that of the curve in Fig. 64, which is schematized from the data of Purdy. This investigator used the following intensity ranges: 10 to 100, 20 to 400, 100 to 400, 100 to 1000, 400 to 2000, and 100 to 2000 photons. He found only three invariables, with such stimuli, but these were substantially independent of the intensities which were compared. The hue shifts were roughly proportional to the *ratio* of the two intensities in the pair. The average values for the stimuli to the invariables gave wave-lengths of 474, 506, and 571 *mμ,* respectively. The spectral psychological primaries were found by the same observer to lie at 476 (blue), 504 (green), and 576 *mμ* (yellow), be-

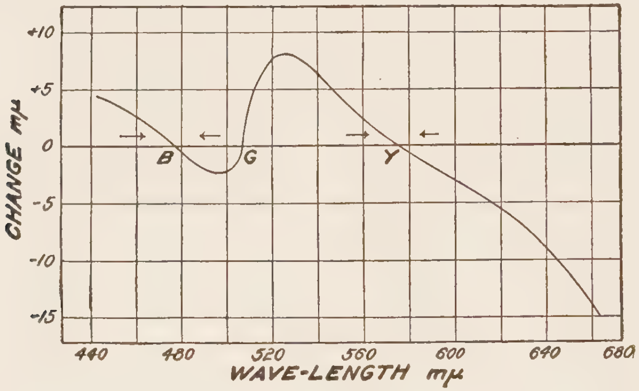


Fig. 64. Diagram to Show the Bezold-Brücke Phenomenon.

This curve shows the shift in apparent wave-length of the various spectral colors, as a consequence of changing the intensity level from 20 to 400 photons. Larger shifts occur with changes over greater intensity ranges, but the curve has the same general form in all cases. The curve is schematized from the data of Purdy.

ing independent of intensity between 10 and 1000 photons. Average deviations in these measurements were about 3.0 $m\mu$. Other investigators have located the invariable hues as follows:

	B	G	Y
Exner[463]	475	508	577 $m\mu$
Voeste[464]	465	496	560 $m\mu$
Langford *	475	493	561 $m\mu$

A study of Fig. 64, in view of the known cyclical relations of the hues, shows that a fourth invariable hue must exist, having a stimulus formed by mixing the stimuli to bluish and reddish spectral colors. Purdy was able to demonstrate this fourth invariable under the following conditions: 420 photons of 629 $m\mu$ mixed with one photon of 427 $m\mu$; and also: 560 photons of 616 $m\mu$ mixed with 3.1 photons of 464 $m\mu$. These two pairs of stimuli yielded identical colors and an exploration of the remainder of the purple series showed no other invariables. According to Purdy, the extra-spectral invariable is not exactly coincident with the psychologically primary red, but is slightly bluish. The discrepancy is not large and might disappear under different conditions of observation or "*Aufgabe.*"

It will be noted that the positions of the invariables correspond approximately with those of the major crossing-points of the three color-mixture curves (Fig. 61). The exact locations of these crossing-points — and, indeed, their total number — depend upon the choice of the color-mixture primaries, and this is commonly arbitrary. Exner proposed to choose the primaries so that the crossing-points would coincide with the positions of the invariables, and found this to be possible. At the crossing-points, two selected color-mixture primaries have equal values, and Purdy has shown that the stimulus conditions for the red invariable correspond to an equality between the green and blue primaries of Exner's curves. It is apparently impossible to demonstrate an invariable for red-blue equality outside of the spectrum.

* Investigations in my laboratory, as yet unpublished.

It is commonly stated that at very high intensities, only yellowish and bluish hues are possible, while at maximal intensities all hues are obliterated by the desaturating tendency.

The general principles presented above for the particular case of spectral colors are followed by all chromas, regardless of the composition of their actual stimuli, whether these be heterogeneous or homogeneous. Chromas which are already unsaturated lose saturation, but at a lower rate than do the more saturated ones. The hues with heterogeneous stimuli alter in the same sense as the corresponding hues in the spectrum. Grays, of course, change in brilliance alone.

IV. CHROMA AS A FUNCTION OF SPATIAL FACTORS

As previously noted, the principles, governing the relations of chroma to the stimulus, which we have thus far presented, apply primarily to vision in the center of the field, with reasonably large areas. The chromatic attributes vary as functions of area and of position, as do the achromatic properties.

314. Areal Functions. — The studies of Donders,[465] Charpentier,[466] and others show that, under certain conditions, the chromatic effect of a stimulus is less with small than with large areas (angular sizes). This effect is greater when the colors are presented against a white background than against a gray of the same brilliance. It is said that a gray can be selected with which the chromatic characteristics arise at the same point at which the given small area becomes visible in any way. Charpentier found, however, that in foveal vision with a dark surrounding field there is always an *areal photochromatic interval.* With gradually increasing size, a pure brilliance experience first appears, followed at a larger area by the chromatic features. The ratio between the absolute and the chromatic threshold areas varied from 4 in the case of the extreme long-wave stimulus to 625 in the case of the short-wave (blue) end of the spectrum.

315. Field Functions. — The influence, upon chromatic characteristics, of position in the visual field, has perhaps received more attention than it deserves in comparison with other visual functions. In general, when a stimulus is moved from the center towards the periphery of the field, the accompanying experience loses chromatic character. The saturation decreases and the range of hue variation is restricted. Stimuli of fixed wave-length composition yield shifts in hue, in accordance with substantially the same law as that which governs the Bezold-Brücke phenomenon. (See Fig. 64.) The psychologically primary red and green change in saturation only, but tend to pass over into a pure gray at an angle with the center which is less than in the case of the blue and yellow. Other hues move towards the blue or the yellow, according as they lie nearer the one or the other of these respective hues, in the chromatic cycle.

The exact laws which govern these effects depend upon the homogeneity, the absolute intensity, and the angular size of the stimulus. The nature of the background and the state of adaptation are also important. Bull,[467] Hess,[468] and others found that when the stimuli were so selected as to yield chromas of equal saturations and brilliance, the angular positions at which red and green disappeared were substantially identical. The same proposition held for yellow and blue. Baird[469] found the stimuli for invariable hue, under change in position within the field, to be a "purplish red" (*i.e.*, an extreme long-wave stimulus plus a small proportion of extreme short-wave), 570 $m\mu$, 420 $m\mu$, and 460 $m\mu$, approximately. Dreher[470] located the homogeneous invariables at 568 $m\mu$, 483 $m\mu$, and 461 $m\mu$. The results of such studies are radically affected by complete scotopic dark adaptation, which brings about an increased desaturation of the chromas for shorter wave-lengths, in the periphery as compared with the center of the field.

Chromatic matches which are established in the foveal region between stimuli differing in wave-length composition, remain good under photopic bright adaptation at all points in the periphery, even when the absolute chromatic effect changes. In general, vision in the semi-periphery tends to be dichromatic, whereas that of the extreme peripheral field is essentially monochromatic. In spite of this fact, the peripheral visibility curve under bright adaptation is photopic in form.

316. Pattern Functions: Chromatic Contrast. — The chromatic consequences of a stimulus are affected to an important degree by excitations in adjacent portions of the visual system. The general law of contrast demands a reciprocal alteration of adjoining processes in such manner as to increase the difference which exists between them without contrast. In the case of the chromatic attributes, these differences may be in the dimensions of hue or saturation, or both. The maximal difference in hue appears to be that between complementaries. The chromatic characteristics are also influenced by conditions of achromatic contrast, whether the former are attributable to the direct action of the stimulus, or to contrast processes. According to Kirschmann,[471] chromatic contrast effects are at a maximum when the brilliance difference between the two areas is at a minimum.

We may consider the laws of chromatic contrast as they apply to a test field, T, with a surrounding (contrast-producing) field, S. Let us suppose the photometric values of the stimuli in the two fields to be identical. If the wave-length compositions of both stimuli are such as to yield a white or a gray, there will, of course, be no contrast effects of any kind. However, if we modify the stimulus for S so as to introduce a certain hue, h, at a definite saturation, s, there will in general be a concomitant chromatic change in T. This latter change will be such as to introduce a hue which is approximately the complementary of h. The saturation of the contrast-produced hue will be less than that of h, but will increase — according to Kirschmann — in proportion to the logarithm of the latter. Pretori and Sachs[472] find that it can be neutralized by changing the stimulus for T in the same manner as that applying to the S stimulus, the two changes being proportional.

When the stimulus for *T* is already such as to yield a chromatic experience, the kind of change which occurs in consequence of chromatic contrast is the same, differentially, as in the case of an initial gray. However, it is necessary to combine this differential effect, in accordance with the principles of color-mixture, with the original chroma. Thus, if the test field already shows a blue, a yellow value in *S* will bring about an increase in blue saturation; while a blue value in *S* will decrease the blue saturation. Red in the surrounding field will throw the hue of the test field towards blue-green, and so on.

A great deal of interest attaches to the influence of areal features of the stimulus upon chromatic contrast. In general, the contrast effect is greater, the smaller the test field and the larger the contrast-inducing area. According to Kirschmann, the effect is proportional to the logarithm of the latter area. If the test area is large, the contrast influence is greater in those portions which are nearer to the inducing field. The action between the two areas is, of course, reciprocal, but follows a principle similar to that governing gravitative action between two bodies; the smaller of the two shows the greatest change. Uniformity of texture between the two areas, and the absence of dark demarcation boundary lines, are favorable to a maximal effect.

When the surrounding field, *S,* is made much brighter than *T,* the colors evoked in the latter are dark and desaturated. They also change chromatically in peculiar ways, so as to pass over into *browns,* olive-greens, and the like. We may consider these changes to be explicable in terms of the same influences which produce black. The exact character of the brown, of course, depends upon the hue value of the stimulus which is involved; chocolate browns are based upon reds, whereas the commoner browns of wood-finishes and the like, rest upon yellows or orange.

It may be noted that chromatic contrast principles can be formulated most conveniently in subjective terms. This indicates the probable truth that they are primarily dependent upon neurological interrelations. The fact that contrast arises with practically the same rapidity as the primary excitations is evidence in the same direction. It is unfortunate, however, that available data provide us with almost no satisfactory specifications of contrast action in terms of wave-length and intensity.

Unfortunately, there is a dearth of data bearing upon the conditions which control purely chromatic patterns in consciousness. Theodore Karwoski, in my laboratory, is now making a study of *chromatic acuity,* with patterns which show uniform brilliance but differences in saturation and hue. The general principles which underlie the relation between the distribution of chromatic stimulus determinants and the chromatic pattern in consciousness are, of course, similar to those which apply to the achromatic features. (*Cf.* pages 84 *ff.,* above, and 186, below.)

V. Chroma as a Function of Temporal Factors

The relationships which obtain between the chromatic attributes of visual experience and the temporal aspects of the stimulus are similar, in general, to those which hold for brilliance, although they are naturally more complicated. Our knowledge of these relationships is quite incomplete and is confused, in some cases, with the corresponding brilliance data.

317. Laws of Rise and Decay. — It is to be presumed that when very brief exposures are concerned, the chromatic attributes are determined by the total exposure (intensity times time), in parallel with the brilliance result. There seems to be no evidence that the chromatic features, as such, are separable from the achromatic ones, by the instrumentality of time. However, there is rather convincing evidence that the rates of rise and decay of the total color experience vary as functions of the wave-length composition of the stimulus. In the classical phenomenon known as Fechner's colors, a white edge, advancing over a black background, is observed to have chromatic fringes similar to those which might be produced by chromatic aberration in a lens system. Helmholtz[473] found that the forward edge appeared reddish, while the rear edge had a bluish tinge, the effect varying somewhat with the stimulus intensity and the speed of movement. Under strong illumination, the forward edge was bluish red and the rearward one, greenish blue. Helmholtz concluded that the rates of rise for red and violet are more rapid than that for green.

Broca and Sulzer[474] found these rates to increase in the order: green, red, blue. More recent studies by Bills,[475] using stimuli carefully matched in photometric value, indicate that the greatest speed occurs in the case of the yellow (at 580 $m\mu$) and the lowest at the blue (463 $m\mu$). The experiments of Ives,[476] upon visual "diffusivity" (*cf.* page 137, above), give clear evidence that there is a progressive increase in the time lag, with respect to the stimulus, of equally bright colors with decreasing wave-length. By moving the stimulus pattern rapidly back and forth before the eyes, he found it possible to bring about a spatial separation of red and blue from a "purple." A similar result was obtained with a yellow evoked by a heterogeneous stimulus ("red" plus "green"), but was absent in the case of a yellow resulting from a homogeneous one. The discrepancies which appear between the findings of different investigators may be attributed to variations in the state of adaptation, the size of stimulus, the intensity level, etc., involving different ratios of photopic to scotopic vision. The safest conclusion seems to be that, under strictly photopic conditions, the rate of rise varies directly as the wave-length when the brilliance values are equal.

It should be noted that these observations apparently do not involve a separation of the chromatic from the achromatic aspects of the color, both of these features being involved in parallel. Brückner and Kirsch[477] have investigated what they call the "chromatic time threshold," by a technique in which a chromatic stimulus is momentarily substituted for an achromatic one. They found that the threshold time must be increased approximately in proportion to the photometric value of the achromatic stimulus.

318. **Chromatic Flicker.** — When two stimuli of equal photometric value, but different wave-length composition, are alternated in the same visual area, a chromatic flicker may appear. It is to be expected that the degree of this flicker will be greater, the greater the given chromatic difference. If the rate of alternation is sufficiently increased, the flicker disappears. Experiment shows that, even with maximal chromatic differences, the frequency which is required for fusion is generally less than that needed to eliminate brilliance flicker. The flicker photometer is based upon this fact, the chromatic differences being obliterated under conditions where the photometric ones are still effective. The chromatic values which result in the state of fusion are identical with those which would be obtained if the same stimulus energies were applied continuously, as in the ordinary color-mixture experiment. This is evidently the chromatic analogue of the Talbot-Plateau law.

It is clear that an infinite number of different chromatic combinations is possible in the flicker experiment. The most interesting ones involve the alternation of a " white " with homogeneous spectral stimuli. My measurements show that the frequency which is required just to eliminate flicker under such conditions has a minimum at 575 $m\mu$, with maxima at both ends of the spectrum. (See Fig. 65.) As previously noted, this curve is probably indicative of the inherent saturations of the spectral chromas. Ives has presented some very careful analyses of the relations between chromatic and achromatic flicker, which account for second order discrepancies between the results of photometry by the method of flicker and that of " direct comparison."

319. **Chromatic Adaptation Phenomena.** — When the exposure to the stimulus is of prolonged duration, large, but relatively slow, changes occur in the chromatic features of the corresponding experience. The phenomena which are observed are different under photopic and scotopic conditions. In general, scotopic dark adaptation tends to bring

about a desaturation of all colors resulting from stimulation of the peripheral retina. This effect increases progressively from the long to the short waves. The reduction of the dark-adapted condition, by exposure to a stimulus, brings about a reverse change. The Purkinje phenomenon and its analogues involve a decrease in the saturation of short-wave chromas, which occurs in strict parallelism with their increasing brilliance.

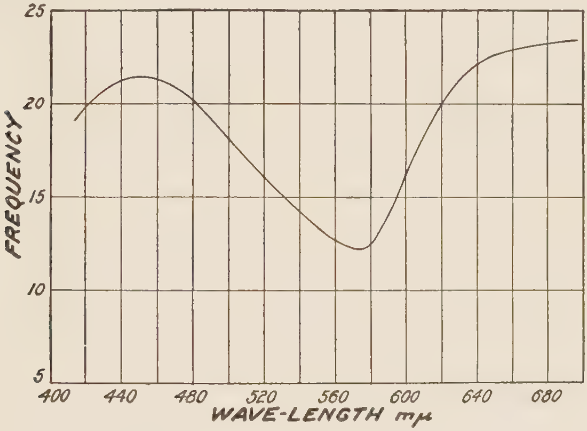


Fig. 65. Flicker-Photometer Frequency as a Function of Wave-length.

Flicker-photometer frequency is defined as the lowest rate of alternation per second of a chromatic stimulus with a "white" which will suffice to eliminate flicker. The curve shows how this varies for spectral stimuli at an intensity level of 1025 photons.

When we are dealing with exclusively photopic factors, as in the center of the visual field, with bright adaptation, the effects are as follow: If the stimulus is allowed to act continuously, the saturation decreases rapidly at first, then more slowly, and finally reaches a steady value. If the initial saturation was very low, a pure gray may result, but, in general, this is not the case, Hering to the contrary notwithstanding. The time required to reach equilibrium conditions is in the neighborhood of ninety seconds, for all stimuli, regardless of wave-length composition or intensity, when a three-degree field is employed. The equilibrium saturation is greater, the greater the initial saturation, but there is a marked reduction in the absolute values and in differences between compared values.

It is a common teaching that, along with these saturation changes, there is a shift in hue, following the same law which applies to the Bezold-Brücke effect. This action seems to be demonstrated very definitely in the quantitative studies of Voeste.[478] However, his experiments inadvertently involved the Bezold-Brücke effect itself, in such a manner as to vitiate his conclusions. New studies by C. H. Langford,[479] in my laboratory, have shown that there is no appreciable shift in hue in consequence of chromatic adaptation; the change is exclusively one in saturation. This fact can be demonstrated in two ways, firstly, by making a hue comparison between an adapted and a non-adapted area without compensating for their subjective brilliance difference. (Such a compensation introduces the Bezold-Brücke effect.) Secondly, by adapting the comparison field with an achromatic stimulus, so that a brilliance equation can be obtained with no difference in stimulus intensities.

320. Complementary After-Images. — If a limited portion of the visual field or system is subjected to chromatic adaptation, the relations between the chromatic attributes and stimulus characteristics suffer a semi-permanent alteration for all stimuli (*Umstimmung*).[480] Thus, if a long-wave stimulus is employed for adaptation, the reduction in the red saturation also involves an increase in the saturation of its complementary, blue-green, when the affected area is tested with a stimulus which is normal for the latter color. This saturation increase can be demonstrated by permitting the "reacting stimulus" to occupy a field which is considerably larger than the affected one. In this case the difference in saturation will be directly observable between the two portions of the field.

This action is not restricted, however, to the complementary stimulus, but applies to all stimuli whatsoever. It may be generalized by saying that the chromatic adaptation operates so as to shift the hue, which is evoked by any stimulus, in the direction of the complementary of the adapting stimulus. This rule obviously includes the latter itself. The principle may be expressed either by saying that a certain amount of complementary is added to the effect of each stimulus, or that the chroma of the primary stimulus is subtracted quantitatively, in a similar manner. It therefore appears that, although there is no hue shift in the primary chroma, this does not forbid such a change in a secondary color which is evoked by a reacting stimulus. If the latter is not identical with the primary one, or with its complementary, there must be an alteration in hue, as well as in saturation. In general, chromas which are nearer the complementary in hue, will be increased in saturation, whereas those which are nearer to the primary will be saturationally decreased.

Chromatic after-effects can also be experienced in the absence of any reacting stimulus, against the dark field of the blind-folded eyes. Under such conditions, a very complex sequence of events is frequently observable: "the flight of colors." The after-image of a very brilliant "white" stimulus tends to go through a series of chromatic phases, and it may also show alternations from bright to dark, corresponding to positive and negative after-image processes. Although these phenomena have been studied extensively, there seems to be no general agreement concerning their normal course.[481]

Recovery. — When the chromatically adapted eye is allowed to rest in an unstimulated condition, it recovers to normal conditions in accordance with laws which are similar, in general, to those which hold for photopic dark adaptation.

321. **Chromatic Dimming and Allied Effects.** — If a chromatically adapted area is subjected to sudden changes in stimulus intensity, some very remarkable effects are produced. A dimming of the primary stimulus can bring out a series of highly saturated chromas, varying in nature with the degree of dimming, the degree of adaptation, and the original stimulus intensity. There is a marked tendency for

purplish chromas to predominate, under these conditions. Theodore Karwoski and I[482] have been studying these phenomena for several years. Frank Allen[483] has shown that chromatic adaptation is responsible for very definite changes in the critical flicker frequency values for spectral stimuli. Both the dimming effect and Allen's observations reveal points of critical transition in the color cycle, corresponding in general form to those which characterize the Bezold-Brücke effect.

A great deal remains to be learned concerning the laws governing chromatic adaptation. In general, it appears that this process changes the proportions of ordinates between the color-mixture elementaries, so that we must compute the colors on the basis of a distorted triangle. However, as we have already noted, chromatic adaptation seems to bring with it no corresponding alteration in the shape of the photopic visibility function, Abney[484] to the contrary notwithstanding.

Section 58

MONOCULAR REFRACTIVE RELATIONS OF CHROMA

322. **General Principles.** — The relations which obtain between chroma and the intraocular refractive processes can be disposed of rather briefly. The chromatic phenomena are, of course, correlated definitely with aspects of radiant energy at all points along the paths of the rays through the ocular media. However, with a few exceptions, the analysis of these correlations provides us with no additional significant information. The geometrical optical principles which apply to the intensity features of the process hold in a similar manner for the chromatic ones. These principles permit us to follow the course of the rays from the corneal surface to the retina, and if the eye were a perfect optical instrument, there would be no complications in

deducing the laws which relate the retinal image to the chromatic features of visual experience.

However, there are certain aberrations in this system which are differential with respect to wave-length and require special consideration as to their influence upon chromatic functions. These include: (1) the selective absorption of the ocular media, in particular that of the yellow spot, (2) fluorescence, (3) chromatic aberration in the main refractive system or in smaller refractive structures, and (4) diffraction by small particles in the media. When the stimulus pattern is complex, so as to present different wave-length constitutions at different points in the field, the general scattering of light in the eye will influence the composition of the stimulus at particular retinal points, so that it departs from objectively determined formulas. We may now consider how some of the chromatic psychophysical functions which we have discussed in the preceding section, may have to be modified for the case of the retinal image, because of these influences.

323. Effects on Hue and Saturation Functions. — The law which associates chroma with the wave-length of a homogeneous stimulus is practically independent of the transmission characteristics of the eye, regarded as an optical instrument, except for the possible action of fluorescence at the shorter wave-lengths. Fluorescence converts homogeneous short-wave energy into heterogeneous radiation having longer wave-lengths. The latter tends, by itself, to evoke a very unsaturated, greenish color; and the fluorescent light combines, in accordance with the principles of color-mixture, with the direct stimulus rays. The result is a partial neutralization of the reddish tinge of the violet, together with an appreciable desaturation. It follows that the retinal version of the spectral chroma scale would show a greater hue variation with respect to wave-length, at the short-wave end, than is exhibited by the corresponding function as determined extraocularly. A true spectral violet should be a more saturated and a more reddish chroma than the color which is normally evoked by the use of a homogeneous short-wave stimulus. Quantitative determinations of the fluorescence in the living human eye appear to be lacking, so that we are unable to compute the nature of this " true violet." However, it seems reasonable to suppose that the kink in the spectral locus at the short-wave end, in the color-mixture triangle, is due to this action; and if we extrapolate this locus approximately in a straight line, we have a basis for computing the range and magnitude of the fluorescence.

The spectral saturation function must also be affected by the action of fluorescence. The results of Jones and Lowry (see page 148, above) reveal no sagging of the saturation at the short-wave end of the spectrum, although I found such an effect in the case of flicker-photometer frequency. (See Fig. 65). It is to be supposed that the retinal function corresponding to Jones and Lowry's measurements would show a considerably augmented saturation value in the extreme violet as compared with that shown in Table VIII.

The failure of the spectral chroma and saturation functions to be influenced by the selective absorption of the ocular media is due to the fact that they are based upon experiments with isolated homogeneous stimuli. Such stimuli can only be altered in intensity by absorption, and the intensity changes are immediately compensated by the technique of the experiments, which requires equal brilliance, a subjective criterion. However, similar studies with heterogeneous stimuli would be affected by selective absorption. Furthermore, when tests with homogeneous stimuli are carried out against backgrounds which are other than dark, the results will be modified by scattered light in the test field, due to the background stimulus. The wave-length composition on the retinal test area will no longer be homogeneous. At the present time, we have no estimates of the magnitude of such ocular " lens flare." It will evidently be proportional to the total flux of light entering the pupil, and hence will involve the area as well as the intensity of the background stimulus.

324. Color-Mixture Functions. — Selective absorption in the ocular media may be expected to have a marked effect upon the chromatic experiences which are elicited by mixtures of different wave-lengths. The laws of color-mixture are expressed in terms of ratios between constituent stimulus intensities, and these ratios are modified by selective absorption. We have already given a representative absorption curve for the average eye in Fig. 47. This curve involves a slight loss of intensity of the long-wave rays, due to the aqueous substance of the eye, as well as a very appreciable selective absorption of the short-waves by the yellow pigment of the *macula lutea.* The former influence is probably quite constant among different individuals, but the latter is extremely variable. Moreover, the yellow pigment has a restricted localization in the center of the retina, so that its influence varies with the position of the stimulus in the field.

The effect of the long-wave absorption will be to decrease the proportion of extreme long-wave stimuli required in mixtures, when the intensities of the components are determined for the retinal image instead of for the external stimulus. A similar action must exist for the short-wave rays. Hering[485] made extensive studies upon the degree and variability of the pigmentation in the human retina, and concluded that individual differences in color-mixture laws are explicable in a great many instances on this basis. He held that differences as great as those between the protanopic and the deuteranopic dichromats could be accounted for in this manner. Sinden's recent determinations of the spectral complementaries show important differences between individual observers,[486] which are of such a nature as to suggest variations in the yellow pigmentation as their cause. These variations should be expected to produce the same effect upon the complementary mixtures as would result from viewing the stimuli through external yellow filters of different densities. Analysis shows that this action should displace the position of the white point in the color-mixture triangle along a straight line in the direction the dominant wave-length for the pigment. Sinden showed that, in fact, with one exception, data from all of his observers conformed to this requirement. The position of the dominant wave-length was located at 572.5 $m\mu$, and Sinden concludes that variations in the ratios of the complementary wave-lengths is primarily attributable to differences in the degree of macular pigmentation. Hence, it would appear that the retinal complementaries are much more invariable than are those which are determined with respect to the external stimulus.

325. **Spatial Effects.** — It is obvious, as already noted, that the localization of the yellow pigment, approximately, within a 4–12 degree central zone, must cause variations in stimulus-experience functions when position in the visual field is altered. These changes will be eliminated by substituting the effective retinal image for the external stimulus, in the functions in question. Hence we may expect some of the retinal functions to resemble the external stimulus functions more closely when they are determined for the mid-periphery of the field than for the center.

Chromatic aberration is responsible for certain spatial chromatic phenomena, which rest upon a variation in the wave-length composition of the retinal image perpendicularly to the boundaries between light and dark areas. The refractive system of the eye is unable to focus different wave-lengths sharply upon the retina at the same time; when one wave-length is sharp, others will form circles or disks of light. Hartridge[487] has shown that, in the case of "white" light, the wave-length which is selected for sharp focussing is probably 580 $m\mu$. He finds that the retinal image of a small point necessarily consists of a "yellow" center, surrounded by a "blue" ring. This condition does not ordinarily receive representation in consciousness, but under special circumstances — as in viewing an incandescent lamp filament through a cobalt glass — the chromatic separation is very evident introspectively. When a small point of light is looked at through a diffraction grating, the resulting color spectrum has a brush shape, in consequence of the ocular chromatic aberration.

There are numerous other minor entoptic phenomena which involve chromatic separation. These include Haidinger's polarization brushes, which comprise a yellow and blue pattern, seen against a bright field of polarized light. This pattern rotates with the plane of polarization, and is attributed to the action of the yellow spot upon the polarized rays.[488] Diffraction, by particles in the cornea and other ocular tissues, yields chromatic halos around bright points of light, viewed against a dark field.[489]

326. **Temporal Features.** — In general, we should not expect the intraocular refractive process to have any important bearing upon temporal psychophysical functions, although it is true that radiant energies of different wavelengths travel at different speeds through refractive media. The absolute velocities are so great, however, that the differences between them have practically no effect upon psychophysical relations. It is conceivable that certain chromatic aberration processes may yield apparently temporal consequences in consciousness. For example, when an intense image boundary is moved rapidly across the retina, the aberration fringes may gain an increased visibility, because of the failure of the local adaptation changes which normally obliterate them. This is a possible explanation of Fechner's colors and the phenomena of apparent differences in "visual diffusivity" observed by Ives. (See pages 137 and 177, above.)

Section 59

MONOCULAR NEUROLOGICAL RELATIONS OF CHROMA

327. **A General View of the Problem.** — A discussion of the retinal and optic-nerve correlatives of hue and saturation brings us definitely into the dangerous domain known as "the theory of color vision." Probably more ingenuity has been expended, with minimum fruitfulness, in this do-

main than in any other field of scientific speculation. Hundreds of different interpretations of the facts have been propounded, all of them consisting essentially in attempts to guess at the hidden neurological mechanism, and its manner of association with visual experience. However, the Young-Helmholtz,[490] the Hering,[491] and the Ladd-Franklin [492] hypotheses continue to receive the greatest amount of attention in text-book expositions. These hypotheses are primarily to be regarded as substantializations of certain rather restricted groups of psychophysical facts, and are quite lacking in contact with modern neurological ideas. In order to render them at all realistic, we must put them " in modern dress." This seems a somewhat safer thing to attempt than the formulation of another " new theory of color vision." It is certainly preferable to the usual review of classical pros and cons. Suggestions made by other visual theorists may be drawn upon freely. Our actual problem, in the present section, is that of examining the present-day probabilities regarding the retinal and neurological correlations of the chromatic attributes, as given in consciousness.

We have already noted that chromatic vision is evolutionarily subsequent to achromatic vision, and that the former is probably developed on the basis of fundamentals which are provided by the latter. It will be recalled that, in our study of the retinal mechanism which probably underlies achromatic response, we have been persuaded of the existence of perhaps two photosensitive substances, contained within the retinal rods and cones, respectively. We have seen how the chemical decomposition of these substances can give rise to optic nerve currents which represent brilliance in terms of impulse frequency. Now, achromatic vision involves the control of only one variable, along any elementary visual path; but the outstanding feature of chromatic vision is the addition of two more independent variables, making a total of three which must be considered. This trifold constitution of the functional system can be formulated in several different ways. Thus, we may deal with brilliance, hue, and saturation; intensity, dominant wave-length, and purity; or red, green, and blue color-mixture elementaries. In any case, if we suppose the visual consciousness to be directly determined by cortical processes alone, we must provide for a trifold conduction path, within each unit visual area.

We may begin with the general postulate that chromatic vision is exclusively photopic and hence is determined by the activities of the retinal cones, only. The scotopic system can be accepted as an additional apparatus, the functions of which are fairly well understood. Attempts by certain modern critics, such as Edridge-Green [493] and Frank Allen,[494] to discredit the duplexity interpretation in this regard, should be rebuked as unwisely iconoclastic. Let us adhere firmly to all ideas which are as well substantiated as are those of the duplexity hypothesis. This means that we are not concerned in the present inquiry with the functions of the rods, nor with scotopic rhodopsin, exception insofar as they adulterate those of the cone system, which it is our purpose to examine.

328. The Three-Component Theory in Modern Form. — Now, the simplest way in which to provide the necessary trifold conduction path is to follow the general plan of the Young-Helmholtz theory, somewhat as follows: Let us suppose that there are actually three different species of retinal cones, each having its own set of private nerve lines to the cortex. These three species of cones may be assumed to contain specific varieties of rhodopsin, having their absorption maxima at separate points in the spectrum, corresponding at least approximately to the maxima of the three color-mixture curves in Fig. 61. If we wish to preserve the integrity of rhodopsin, as a chemical substance, we may suppose that the displacements of the curves are referable to three different optical densities in the cone substance, or to some process of interference due to the complex refractive and reflecting processes, such as undoubtedly occur in the terminal segments of the receptor cells.[495] In any event, the mode of response of each cone species can then be regarded in exactly the same manner as the brilliance-intensity functions.

It is natural to assume that the three kinds of cones are interspersed more or less uniformly over the retinal area, to form a statistical mosaic. We have seen that photopic, as well as scotopic, brilliance rests upon an areal summation of nerve pulse frequencies over a considerable number of simultaneously operative receptors, although the number decreases with increasing stimulus intensity. Such a fusion of process between adjacent conducting lines can be relied upon to yield chromatic cancellation or mixture within small areas, even when there is concomitant achromatic discrimination. The studies of Hartridge on the chromatic aberration of the eye, already cited above, show that chromatic fusion of this sort must actually occur, regardless of the assumed differentiation of cone response. Quantitative investigations of pure chromatic visual acuity have not been reported, but common observation makes it almost certain that they will show values which are much lower than are those for achromatic acuity. The chromatic "unit area" may be assumed to average at least three times greater than the corresponding achromatic "unit area." Hence, there is little reason to expect that "white" surfaces will appear as fine-grained chromatic mosaics or that stars will twinkle kaleidoscopically.[496] Star images will be smeared over a considerable number of cones by the aberrations of the eye, and will remain centralized on a single cone only for very brief intervals of time, owing to the instability of fixation.

In general, all of the facts of color-mixture, or the control of chromatic attributes by the wave-length composition of the stimulus, whether homogeneous or heterogeneous, can be explained adequately on the basis of such a scheme. We can harmonize the relationships between these attributes and brilliance values in the following manner: Conduction along the optic-nerve fibres, corresponding to each cone species, of course proceeds in terms of substantially regular series of all-or-none impulses, and the brilliance magnitude is determined by the frequency of these impulses.

However, when the three kinds of cones are stimulated by radiant energy having the composition of sunlight, the long-wave cones (for red) yield a lower frequency than do the mid-wave ones (for green), while the short-wave cones (for blue or violet) generate a very low frequency, say, one one-hundredth the value for the mid-wave species. Nevertheless, this is the ratio of frequencies which operates in the cortex to give an achromatic color. However, this relationship is not absolutely fixed, being subject to change under the influence of "memory color" or "transformation" cues.

The almost perfect symmetry of the retinal visibility curve can be explained in conformity with this scheme in several different ways. In the first place, the standard visibility function is itself a statistical average of a large number of individual curves. Any one of the latter may show a marked departure from symmetry. However, it is entirely conceivable that the three response curves should add to form a substantially symmetrical function since, firstly, the "red" and "green" maxima are very close together, and secondly, the contribution of the "violet" curve is practically negligible. The color excitation curves, as they are ordinarily plotted, are necessarily of such a form that they will summate to yield the visibility curve, when the appropriate coefficients are applied. This makes them individually asymmetrical, but asymmetry is characteristic of absorption functions in general.

329. Easy Explanations by the Three Component Theory. — In terms of the above conceptions, hue and saturation must be determined by the *ratios* of the impulse frequencies, received or transmitted in a "unit area," the absolute or total frequency being responsible for the brilliance. Let us assume the ratio, $F_R : F_G : F_V$, for white. If any one of these frequencies is reduced, while the others remain constant, it will play no part in the regulation of the hue. The latter will then be determined by the ratio of the other two frequencies. If two frequencies are reduced in the same proportion, the hue will be that which is characteristic of the process represented by the remaining frequency. The ratio of the dominant frequency, or frequencies, to the remaining ones will regulate the saturation. Dominancy is of course relative to the basic ratio for white, and the indicated types of ratio variation may be brought about by increases as well as by decreases, and at any absolute frequency level.

The failure of this system, on its surface, to account for the uniqueness of the psychologically primary hues — red, yellow, green, and blue — is not a strong argument against it, since the direct parallels of these primaries are to be looked for in the cortex. Introspective distinctions are most likely to find their simplest correlates in the cerebral system. The latter must provide some definite mechanism for dealing with the frequency ratios which we have been considering, and the mechanism in question may well operate as follows: The short-wave process by itself yields blue, the mid-wave yields green, and the long-wave yields red. Combination of the last two in the ratio, $F_R/F_G = 1$, yields yellow, while concurrence of the yellow resultant with the short-wave process, in the ratio previously specified, gives white or gray. Black accompanies zero frequency along all of the fibres, being characteristic of the intrinsic activity or state of the cortical visual field by itself. This scheme has the logical form of the Ladd-Franklin theory, in its manner of dealing with the psychological primaries. In general, it seems unlikely that the cortical foundations of the hues can consist merely in the constellations of frequencies which arrive from the sense-organ. These constellations must operate through a definite mechanism to release new substances, or activities, which may be as numerous and unique as circumstances demand.

The reappearance of reddishness in conjunction with short-wave stimulation can be attributed to a second rise of the long-wave process at its " second harmonic." This is a familiar property of absorbing pigments; practically all red-absorbing dyes are also strongly absorptive of violet, a necessary property of any pigment which is " green," rather than "blue-green." This second rise appears automatically in the color-mixture diagram, if we select the short-wave primary at the blue point in the spectrum.

The manner in which chroma varies as a function of wave-length is accounted for, qualitatively, by the assumption of three overlapping chromatic response functions, similar to those of Fig. 61. The most rapid variation, the greatest wave-length sensitivity, should coincide with the loci of maximal difference between the slopes of the curves. The sensibility should be particularly great where two curves show slopes in opposite directions, one increasing as the other decreases. This occurs in the yellow and the blue-green. The minor maxima are to be attributed to the initial rise of the red response and the fall of the violet or blue. The distribution of saturation in the color spectrum is also explained, either by the disposition of the spectral locus with respect to the white point, in the color-mixture triangle, or by the degree of triple overlap of the curves of Fig. 61. Complementary relationships, being special cases of color-mixture, must be explained quantitatively by the same constructions. It should be borne in mind that the familiar color-excitation curves are based upon more or less arbitrary selections of primaries, so that it is legitimate to recompute them in such a manner as to secure the best possible quantitative explanations of the hue and saturation functions.

330. Difficulties Encountered by the Three Component Theory. — At this point in the argument, however, we begin to encounter some apparent difficulties, if we assume color-mixture functions such as those which have been presented by Abney or by König and Dieterici. Helmholtz [497] assumed that the three functions overlap to a very considerable degree, over the entire spectrum, but Abney [498] supposes that the red is excited in isolation in the extreme long-wave region, while it is absent in the extreme short-wave position. If this were true, chromatic adaptation to the long-waves should yield no increase in the saturation of the blue-green which is evoked by their complementary. As a matter of fact, there is a large saturation increment in all such experiments, regardless of the wave-length of the adaptation stimulus. Only by means of experiments of this sort can we actually ascertain the probable amount of overlap. If this latter is assumed to be very large, we can account for the failure of specific chromatic adaptation to produce an appreciable change in the form of the visibility curve. However, the greater the overlap, the smaller become the differences, between the three processs, upon which the chromatic attributes must depend.

The changes in hue and saturation which occur with increasing stimulus intensity are readily accounted for. The relation between the nerve current frequency and the stimulus, for each species of cone, presumably follows a law of the Fechnerian (our so-called Fechner function) type, although the constants of the law may well be different in each case. Hence, it is to be expected that the more strongly excited cones will show a slower increase in nerve pulse frequency, with increasing stimulus intensity, than will the more weakly excited ones. Thus, under such conditions, there must be a loss of saturation with any chromatic stimulus, this being more marked, the greater the initial saturation. The shift in hue is to be attributed to differences between the constants of the Fechner function for the several receptor processes, or in their basal excitation potentials. The trend towards the blue and the yellow can perhaps be explained in terms of the very low relative activity of the " blue " cones which is required to yield a neutral mixture. This should mean, not only a greater resistance of blue and its complementary to obliteration by intensity, but also a higher " diffusivity " in Ives' sense. (See pages 137–138, above.) The absolute amount of change in process which is required of the blue to yield a specific chromatic effect would be less than in the case of the red and the green, and hence might be expected to occur in a shorter time.

The most serious difficulty with these views appears when we try to harmonize them with the absence of hue shift under chromatic adaptation. The saturation loss, under these conditions, follows at once from the assumption of extensive mutual overlap between the three excitation functions. Adaptation should maximally reduce the processes which are most strongly aroused, thus tending to push the excitation ratio towards that for a gray. For this same reason, we should expect a spectral red to shift towards the yellow under bright adaptation, since the "red" cones should suffer a greater reduction of process than the "green" cones. The only way out of this difficulty seems to lie in the assumption that, although the absolute sensitivity loss of the "red" cones is greater than that of the "green" cones, the ratio of their processes — as represented by the respective nerve current frequencies — remains unchanged. This means that the law which governs hue is different from that which controls saturation, a proposition which is not at all unlikely.

In order to account for the possibility of negative and complementary after-images, against the idio-retinal light, we must suppose that the three species of cones have a self-activity even in the absence of external stimuli. We have already considered the basis and probability of this process in our discussion of the psychophysiology of brilliance. Since the idio-retinal light is normally gray, we must conclude that the self-activity involves an excitation of the three paths of nerve conduction in the ratio required to yield "white." This means that the self-excitation of the "blue" cones is very low compared with that of the "red" and "green" cones. When an external stimulus is operative, its effect is added to the self-activity, but does not obliterate the latter. Since a solar distribution of energy yields a gray or white at all intensities, we must suppose that the excitation ratios of the three cone processes increase in the same proportions from the lowest to the highest values, under the action of such a stimulus. These facts lead us to conclude that the concentrations of the three specific absorptive substances are approximately in the same ratio as the ratio between the corresponding nerve currents to yield white.

331. Contrast and Color-Blindness According to the Three Component Theory. — The phenomena of simultaneous chromatic contrast are probably to be attributed primarily to cortical rather than to retinal or conductional readjustments. However, the mechanism of the diffusion of end-products in the retina, which we have already discussed in connection with the theory of brilliance contrast, will yield complementary contrast chromas, if the end-products are specific to the three processes.[499] The variation of hue and saturation, as functions of position in the visual field, is to be attributed primarily to differences between the chromatic mechanisms at corresponding points in the cortical area. The cortical receivers for the " red " and " green " nerve currents become very scarce in the mid-peripheral field, while those for " yellow " and " blue " are practically absent in the extreme periphery. There may be parallel changes in the complexity of the receptor and conductional systems, although the constancy of the photopic visibility curve and of chromatic matches over the whole field suggests that the receptor mechanism, at any rate, is identical for all parts of the retina.

The commoner forms of color-blindness can readily be explained in terms of the above general scheme. Protanopia, or red-blindness, would seem to rest upon an absence of the " red " cones, combined with a non-functional condition of the " red " and " green " receivers in the cortex. Deuteranopia, or green-blindness, may depend upon this cortical condition, alone, since the visibility curve is substantially the same as for trichromatic vision. These forms of color-blindness are definitely hereditary and hence probably reveal certain lines of cleavage in the genetic structure of the visual mechanism. Other types, referable primarily to pathological forces, may be due to quantitatively variable alterations in any component in the complex system, either so as to produce excessive or deficient activity. Thus, in santonin poisoning the " yellow " cortical receiver is presumably overstimulated. Tritanopia, or blue-blindness, can be referred to disease or weakness of the " blue " retinal cones. It is frequently associated with detachment of the retina, which may affect these cones more readily than the others, because of the low potential of their activity. Anomalous trichromatism is to be attributed to minor variations similar in general character to those which underlie protanopia and deuteranopia.

332. The Hering Theory In Modern Form.— The Hering theory is similar to that of Young and Helmholtz in that it employs three independent variables. However, the relations of these variables to visual experience and to the action of the stimulus are conceived in a radically different manner. In the first place, they can have negative as well as positive values. Secondly, there is a more direct connection between the aspects of these variables and the psychologically primary colors than in the case of the Young-Helmholtz theory. These relationships can be schematized by means of a color-mixture triangle which has one apex at white, another at blue, and the third at green. Yellowish and purplish chromas must then be represented by negative values (outside of the triangle) of the blue and green elementaries, respectively. Color-mixture data can be plotted with respect to such a triangle, just as legitimately as within the triangle which corresponds to the Helmholtz assumptions. Variations, positive or negative, in the white factor must occur perpendicularly to the plane of the triangle, and correspond to pure changes in brilliance. Hering assumes that the brilliance which goes with a zero value of the white factor consists in a medium gray, negative values representing variations towards black, and positive ones changes in the direction of white.

In its original formulation, the Hering hypothesis is unduly lacking in definiteness and is difficult to accept in the light of modern views regarding the neural processes. However, we may recast it somewhat as follows: We assume, again, the existence of three different species of cones. One of these contains cone rhodopsin, which is decomposed by different wave-lengths in accordance with the photopic visibility curve, yielding, by itself, a purely achromatic color which varies in brilliance with the frequency of the corresponding nerve currents. This cone system, together with the other two systems, may be supposed to show a considerable degree of self-activity, corresponding to the idio-retinal light. A depression of the excitation of the brilliance cones below this level can occur only through the influence of bright adaptation or contrast. However, in the case of the other two species of cones, we may assume that either depression or augmentation of process may occur in consequence of the action of particular kinds of radiant energy. One set of cones, which we may call the yellow-blue, have their processes increased by the action of wave-lengths longer than about 505 $m\mu$ and decreased by those which are shorter. The other set, the red-green cones, suffers augmentation by wave-lengths greater than about 575 $m\mu$ and less than 478 $m\mu$, but which is depressed by wave lengths in the intermediate band of the spectrum.

We may furthermore assume that the contribution which is made to the total brilliance by the activities of the chromatic cones is very small compared with that due to the achromatic ones. This will be attributable to a generally low frequency in the resulting nerve currents. However, this frequency, such as it is, summates with that of the achromatic system, at any time, to yield the total brilliance-determinant in the cortex. When the nerve currents along the fibres of the two chromatic systems are at their normal, rest, values the accompanying color experience is entirely achromatic. However, if those in the yellow-blue system are increased, the experience is altered in the direction of yellow, the saturation being greater the greater the augmentation. Depression of these nerve currents, on the other hand, yields blue, which is saturated in proportion to the extent of the decrease. The red-green system operates in an entirely analogous manner. When the chromatic cones are acted upon by radiant energy having the distribution of sunlight, there is an equilibrium between the excitatory and depressive influences, so that no change in process occurs, the increase in brilliance being wholly referable to the response of the achromatic cones.

This scheme, some of the details of which were suggested by the theory of Forbes,[500] is rather less plausible than the one which we have developed on the basis of the Young-Helmholtz doctrine. Chemical processes which are enhanced by certain wave-lengths and inhibited by others are known, but are not very common. However, the view fits certain of the psychophysiological data more satisfactorily than does the alternative hypothesis. It throws the burden of the brilliance process almost entirely upon one species of cones, thus accounting readily for the relative independence of the brilliance-stimulus function with respect to chromatic differences. However, at the same time, it leads us to expect a slight contribution (specific brightness of colors, according to Hering) of brilliance effect from the chromatic system, the extent of this contribution varying with the type of process which is involved. We might reasonably look for a maximal action of this sort in connection with flicker and dimming procedures in the presence of strong achromatic bright adaptation. We should expect to find very little evidence of brilliance adaptation that is specific for particular wave-lengths, and this expectation is in harmony with the facts. The extreme differences between the chroma-brilliance coefficients of different wave-lengths are attributable to the accidental relationships between the achromatic and the chromatic response functions, as plotted on the wave-length scale.

Color-mixture laws, spectral chroma scale data, the relative saturations of spectral chromas, negative and complementary after-images, and numerous other phenomena can be explained in terms of this modernized Hering theory just as readily as they are handled by the Helmholtz type of hypothesis. However, the explanation of the various types of color-blindness introduces complications. Dichromatism, in general, can be referred to the absence of the red-green system of cones, but the difference between protanopia and deuteranopia must rest upon some other concomitant variation, the identity of which is not so evident as in the case of the Helmholtz type of theory. There may be a change in the shape of the achromatic response curve, *per se,* or some difference between the absorption characteristics of the ocular media, as claimed by Hering. The absence of hue shift, under chromatic adaptation, however, constitutes the greatest difficulty, just as for the Helmholtz doctrine.

333. The Ladd-Franklin Theory and Nerve Current Modulation. — Mrs. Ladd-Franklin's view that the photopic receptor process involves three different forms of decomposition of a single chemical substance obviously does not lend itself to a three-cone interpretation. If her doctrine is to prevail as a realistic description of the retinal response, we must suppose that all three of the required variables can be represented simultaneously by transmission along a single nerve fibre. In the present state of our knowledge, we cannot deny that we may eventually be forced to assume such transmission, in spite of its seeming incompatibility with the modern conception of nerve conduction. Conclusive evidence that complete chromatic vision can be subserved by the response of a single foveal cone, and its attached optic nerve path, would seem to necessitate some such line of thought as the following:

All of the cones are actually alike, and their brilliance response is due to the decomposition of cone rhodopsin, which controls the frequency of the corresponding nerve currents. However, in addition to the rhodopsin, there are at least two other photosensitive substances or structures, which respond selectively to wave-length, with maxima in spectral positions different from that for the rhodopsin. The effect of such response is to *modulate* the nerve currents in two characteristic ways. I use the term, *modulate*, here, in a sense analogous with that in which it is employed in the theory of the radio-telephone, to imply the introduction of a low frequency variation into a medium provided by a higher frequency one. In the case of the nerve current, such modulation cannot be continuous or smoothly graded, but must comply with the all-or-none principle. This means that it must consist in the production of variable gaps in an otherwise regular sequence of pulses. Two independent modes of variation could exist very simply, if the lengths of the gaps and of the filled intervals, respectively, were separately regulated. Many other systems of modulation are conceivable. The control of modulation might be assigned to the second reaction of Hecht's scheme, supposing that this is separately affected by wave-length composition in the case of the cones, but not in that of the rods. If we accept the suggestion that this second process is actually the response of the neural membrane, we may be impressed by the idea that the latter is peculiarly fitted to regulate the rhythm of the nerve current. It is quite conceivable that the general scheme of such a single cone system should comply with that of Mrs. Ladd-Franklin's hypothesis.

In general, we may note that the notion of nerve current modulation enables us to superimpose chromatic variables upon the achromatic (brilliance) one in a manner which harmonizes with many psychophysical data. Chromatic attributes thus become conditional upon the preëxistence of the achromatic one, and yet may cause no change in the values of the latter, when introduced — just as in the case of the ordinary system of radio-telephone modulation. The two independent modes of modulation can readily be conceived so that they naturally tend to neutralize each other and to reconstitute the unmodulated disturbance of achromatic response with proper combinations of wave-lengths. However, space forbids that we should develop all of the possibilities of this rather too speculative hypothesis in the present book. As an alternative to the modulation idea, we might consider the suggestion that chromatic attributes may be carried in the optic nerve currents by variable phase relations between adjacent impulses, in a three-fold system. This would permit all of the nerve currents to be alike, *per se,* and to support a purely achromatic effect in isolation, but to mediate a chromatic result in combination. However, it it is difficult to imagine how such a phase relationship could be controlled. Differences in the points of initiation of the impulse due to possible interference phenomena in the cone segments would be too minute to yield any appreciable phase shifts of the impulses, as a function of wave-length.

We may note that the domain of color sensation theory, as portrayed in the above discussion, should prove a veritable bonanza for any research worker with a fruitful imagination and an equipment for quantitative investigation. A few crucial experiments should enable us to establish, firstly, whether any form of the three-cone hypothesis is tenable, and, secondly, whether either the Young-Helmholtz or the Hering schemata are applicable to this notion, if the answer to the first question is affirmative. It is quite likely that some formulation which is rather different from either of these schemes will emerge from properly chosen lines of experimental study. In any event, we must be very careful to bear in mind the serial complexity of the propagational mechanism which is involved, and its subjection to the principles of nerve excitation.

Section 60

BINOCULAR SENSORY RELATIONSHIPS

Up to the present point, our discussion of sensory relationships in vision has been confined to a consideration of factors which are contained in a single eye, or its attached conducting fibres. Of course, the two eye responses are essentially similar, considered singly, but there are certain features of consciousness which rest primarily upon *relations* between them. Insofar as the factors which enter into these relations are exclusively contained in the double afferent arc, they should obviously be classified as sensory. Binocular sensory functions have the form: $\psi = f(\phi_l, \phi_r)$, where ψ represents the appropriate attributes of the visual consciousness, and ϕ_l and ϕ_r stand for the left and right ocular (or neural) variables, respectively.

334. **Corresponding Ocular Regions.** — It is clear that our doctrine of corresponding rays, or ocular angular positions, as presented in the sections on visual perception (Volume I), can be translated immediately into a theory of

corresponding retinal points, or corresponding receptors and optic nerve conductors. Indeed, it is common practice to express the general theory in question in terms of the retinal, rather than of the extra-ocular, positions. "Corresponding points" are ordinarily defined as points which would be coincident if the two retinas could be placed, one over the other, with the foveas and apparent vertical axes in approximate register. However, little additional insight is gained by a transformation of the objective corresponding angular positions into corresponding retinal points, although we cannot doubt that the latter is a more fundamental specification of the psychophysical realties. An even more basic conception would deal with corresponding optic nerve fibres, or cortical receiver elements. We may delay a further analysis of these problems until we can consider the manner of combination of the corresponding conduction processes in the cortex. This is a matter of "cerebration" rather than of "perception" or "sensation," in our meanings of these terms.

335. **Retinal Rivalry and Binocular Color-Mixture.** — When corresponding areas of the two retinas are stimulated simultaneously, the resulting color attributes are nearly the same as those which follow from monocular stimulation, if the two stimuli are substantially identical and the two eye systems are in the same physiological condition. There is no summation of brightnesses or of saturation, at least when the experience is of the "film color" species. However, changes in depth position are frequently accompanied by alterations in saturation, even when the wave-length compositions of the stimuli remain constant. When the stimuli for the two eyes are different, either in intensity or composition or both, there is a tendency for the resulting experience to be intermediate between those would be given, normally, by the right and the left eye stimuli, taken singly. This means that if the former would normally yield, say, a brilliant white, and the latter a gray, the addition of the stimulus to the gray to that for the white must actually decrease the experiential brilliance. This fact is known as

Fechner's Paradox.[501] If the two stimuli are such as would produce, separately, colors which differ in chroma, there may be either binocular color-mixture or "retinal rivalry."

Retinal rivalry consists in an alternation, in experience, between the colors or patterns due to the right and the left eye processes, respectively. The tendency for such rivalry to occur is greater, the greater the difference between the two stimuli, or their normal monocular consequences, in any dimension. These dimensions may correspond to brilliance, hue, saturation, or form. Investigators disagree as to the degree of the chromatic differences which are compatible with binocular fusion, or the absence of rivalry; but it seems certain that these differences may sometimes be maximal. "Red" and "green" may yield a yellow, while complementaries give white.[502] This evidently means that the cortex possesses self-sufficient arrangements for producing these psychological primaries from separate nerve currents which normally represent the corresponding color-mixture constituents. The alternation which exists in rivalry may occur separately, or out of synchronism, for different portions of the visual field.

336. Binocular Flicker Effects. — The very interesting experiments of Sherrington[503] show that, when flickering stimuli are applied to the separate eyes in such a manner as to dovetail one series of exposures with the dark intervals between the other series, the critical flicker frequency is substantially the same as for monocular stimulation. This seems to indicate that the locus of the fusion mechanism is in the afferent arc, rather than in the cortex. The very slight reduction in critical frequency which is actually demonstrable represents a small contribution of inertia by the cortex, which is apparently of a different order of magnitude from that of the sensory arc.

Frank Allen[504] has shown that if one eye is adapted to any stimulus — excepting certain unique wave-length compositions — there is an increase in the critical flicker frequency for spectral stimuli which are applied to the other eye, especially when the latter is not dark adapted. However, this increase is not uniform, but exhibits maxima at both ends, and in the middle, of the spectrum. Six, so-called "equilibrium stimuli," corresponding to wave-lengths 660, 570, 520, 505, 580, and 525 $m\mu$, respectively, produce no effect. Allen's view that these phenomena involve a "reflex" interaction between the two eyes, as such, is probably erroneous, a simpler explanation lying in the common cortical basis of the two eye effects. This is, of course, a general requirement for practically all binocularly conditioned phenomena. Although Allen interprets his results in terms of brilliance determinants, it seems almost certain that they are actually referable to purely chromatic variables, and should throw particular light upon the nature of the cortical chromatic relationships.

Chapter XV

Auditory Sensation

Section 61

COMPONENT AUDITORY SENSATION

337. Definition of the Problem. — The problem of auditory sensation may be defined as that of the relationship obtaining between experience and the various stages of the afferent auditory response arc. It is more or less arbitrary as to exactly where we consider this arc to begin or end. The most convenient point at which to place its beginning is probably within the external auditory canal (meatus) ; and its ending is to be located somewhere in the auditory projection area of the cerebral cortex. Defined in this manner, the afferent arc of course comprises a very large number of sub-stages, the relationships of which to experience should be considered separately, so far as is possible. Unfortunately, our knowledge of the details of the majority of such relations is very inadequate at the present time, being confined to the stimulus, some semi-hypothetical notions in relation to the operation of the sense-organ, and some very hypothetical ones involving the afferent nerve conduction. The characteristics of auditory experience have been discussed in Volume I. (See also Note B, below.)

We may consider, first, the psychophysiological relationships which obtain between *components* of auditory experience and various aspects of the *stimulus*. The latter may be identified, in the auditory case, with the sound waves, as they exist within the external auditory meatus and act upon the eardrum, or tympanum. With certain reservations, which we have considered under the heading of auditory perception, the characteristics of the sound waves at this point correspond rather closely to those of the same waves as they are emitted by the source and propagated through the intervening space. There are, of course, normally two auditory stimuli to be considered, one for each ear, and these are not necessarily exactly similar, even at the same moment. We may obviously deal with the problem of auditory sensation either for normal *binaural,* or for experimental monaural conditions.

338. Nature of the Auditory Stimulus. — From a purely physical standpoint, the auditory stimulus consists of a rapid variation in barometric, or atmospheric, pressure within the meatus, this pressure alternation being accompanied by corresponding movements of the air molecules to create the successive phases of condensation and rarefaction. We have already noted that, as a rule, such pressure changes follow a complex pattern in time, but can be analyzed into a sum of simple harmonic variations, having particular frequencies and amplitudes. This analysis can be carried out mathematically, when we know the law which determines the vibrational form as a function of the time. It can also be accomplished by use of a machine, known as an harmonic analyzer, starting with a graphical representation of the wave form. When the vibration is periodic, or repeats itself precisely after a given interval of time, the number of simple harmonic constituents is finite; but if it is aperiodic, the number will be infinite. On the basis of such an harmonic analysis, we can plot an *auditory distribution curve,* such as that shown in Fig. 66, which represents the pressure amplitude for each component in a complex sound.[505] A representation of this sort is known as a pressure spectrum. As a rule, such spectra are made up of discrete lines, but in the case of aperiodic vibrations, they may be continuous, and be represented by a curve, as in the case of the commonest visual stimuli.

Sound intensity, as a general dimension, can be expressed in a number of different ways. From the general physical standpoint, the most significant measure of intensity is in

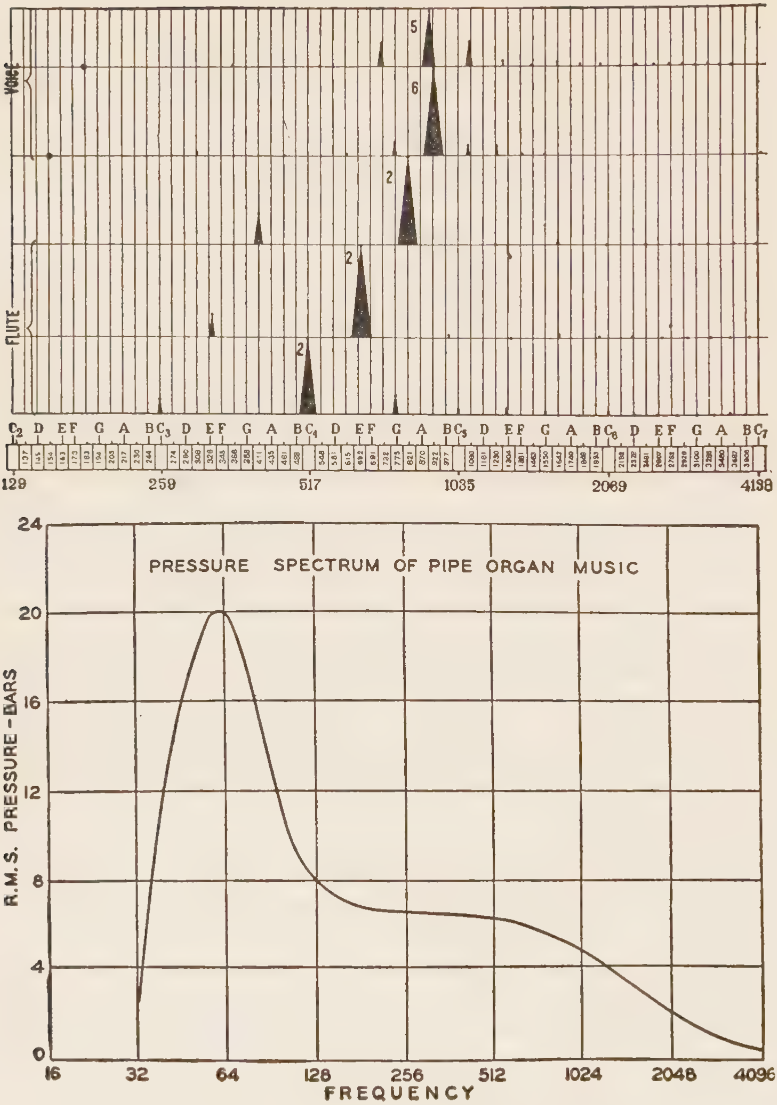


FIG. 66. EXAMPLES OF ACOUSTIC DISTRIBUTION CURVES.

The upper diagram in this figure represents the distribution of acoustic pressures in several specific voice and flute sounds. The lower diagram shows the average distribution of pressure in organ music, as ordinarily played. (*From Miller: The Science of Musical Sounds, Macmillan; and Fletcher: Speech and Hearing.*)

terms of *energy* units or the closely related units of *power*. Energy is measured in ergs, just as in the case of radiant energy, and power in ergs per second, or in watts, the rate of flow of energy (say, into the external auditory canal). In the auditory case, as in the visual, a unit of surface is also involved, since the amount of power which is applied to the tympanum depends upon its area. However, the fact that the area in question is invariable enables us to neglect it except where absolute measurements are required. Sound intensity can also conveniently be expressed in terms of *amplitude*, which may stand either for the distances through which the air particles move or for the maximal increase or decrease of the pressure with respect to the given atmospheric value. The latter method of expression is preferred on account of its definite dynamic significance, and is naturally in terms of *dynes per square centimeter*. Although it is, strictly speaking, a pressure *variation*, or difference, it can be treated as absolute because the undisturbed tympanum is subject to normal atmospheric pressure from both sides.

Up to quite recent times, it has been impossible to make accurate measurements of sound energies or amplitudes, but instruments such as D. C. Miller's phonodeik, the condenser transmitter, the vacuum tube oscillator and the thermophone have finally provided the requisite means.

339. **Acoustic Loudness.** — Telephone or transmission engineers have defined a concept of loudness, for the purposes of their business, which is of especial interest because of its psychophysiological character. It is definitely the acoustic analogue of photometric intensity in the visual instance. Naturally, it cannot be identified with loudness in the purely subjective sense, and in order to distinguish between the two concepts, we may designate it as *acoustic loudness*. The scale of acoustic loudnesses[506] is founded upon the psychical loudness of a 700 cycle note having a R. M. S. pressure amplitude of 0.001 dynes in the external auditory canal. This is the normal absolute threshold for the frequency in question, which is close to the best representative one for speech. Tones, noises or vocables corre-

sponding to other frequencies, or frequency compositions, are to be equated in subjective loudness to this standard, or some multiple thereof, and then defined as of equal loudness. Such a heterotonal equation of loudnesses is analogous to the heterochromatic equations of brightness in photometry.

The scale of acoustic loudnesses is logarithmic with respect to the energy, for any single frequency, the value being taken as ten times the common logarithm of the energy, expressed in terms of the threshold loudness as a unit. Acoustic loudness is a linear function of subjective loudness over the range of intensities for which Fechner's law holds, but not under other conditions. It is proportional to the so-called "transmission unit" or "decibel" of telephone engineering, with an appropriate additive or subtractive factor; and is approximately in inverse proportion to the number of miles of standard cable over which a telephonic audio signal has been transmitted.

340. Method of Analysis. — We may first consider the relationships which are involved when only a single ear is stimulated, or which are not altered when the second ear is added. In discussing these relations, it will conduce to clearness to consider them as modes of determination of the various classes and attributes of auditory experience, taken in a subjectively determined order: (1) tones, as to (a) loudness, (b) pitch, (c) brightness, (d) volume, (e) octave quality; (2) vocables, as to (a) vocality, (b) tonal attributes, as above; and (3) noises, as to (a) quality, and (b) tonal attributes. These may be treated separately in relation to each of the separable features of the stimulus: (a) frequency, (b) amplitude, (c) composition, (d) phase, etc. Our actual experimental procedure will force us to vary the stimulus characteristics individually and to accept the complex changes in all of the experience attributes which result, but we can abstract from such of the latter as do not concern us in the given experiment.

341. Loudness as a Function of Frequency. — Suppose that we apply, to the tympanum, a pure harmonic vibration of controllable amplitude and frequency composition. First, let us hold the energy of the stimulus constant and vary the frequency from zero to a very high value. We find that below about 16 vibrations per second there is no auditory accompaniment in consciousness, but that, as the frequency is further increased, a tone appears, having at first a very low pitch and minimal loudness, increasing both in pitch and in loudness, as the frequency progresses. The pitch continues to rise, but at a frequency of about 2050 per second the loudness begins to drop off, becoming zero again at about 20,000. The limits depend upon the exact value at which the energy, or the amplitude, is held constant. Thus, at a constant amplitude of 0.01 dynes per square centimeter, the limits are 200 and 12,600 cycles per second.[507] In this

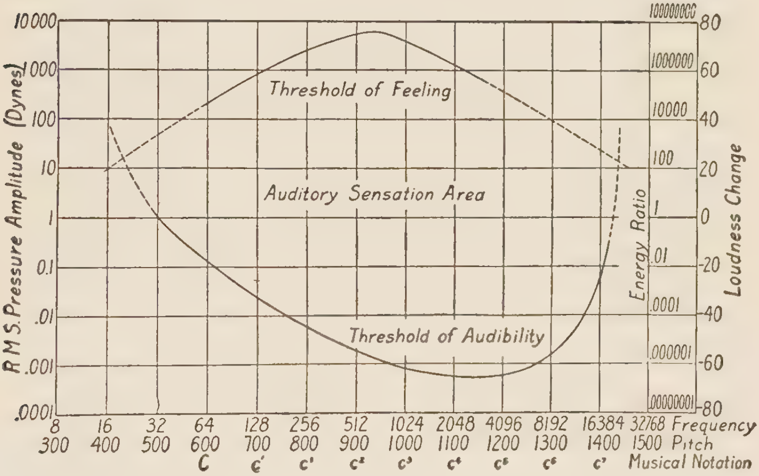


FIG. 67. AUDIBILITY AND TACTILE THRESHOLDS AS FUNCTIONS OF ACOUSTIC FREQUENCY.

The two curves in the figure show the minimal pressure, in bars (dynes per sq. cm.), required for auditory or tactile response, respectively, at various frequencies. Atmospheric pressure (about 14 pounds per square inch) is approximately 1,000,000 bars, so that the lowest audibility threshold corresponds to a change in pressure upon the eardrum of about a millionth part. The figure also shows the relations of energy ratios and loudness to pressure values, and of pitch and musical notation to frequency. (*Fletcher: Bell System Technical Journal.*)

way, we demonstrate that both pitch and loudness are functions of frequency.

Considering, first, loudness: if we wish to secure a quantitative expression of its relationship to frequency, we can

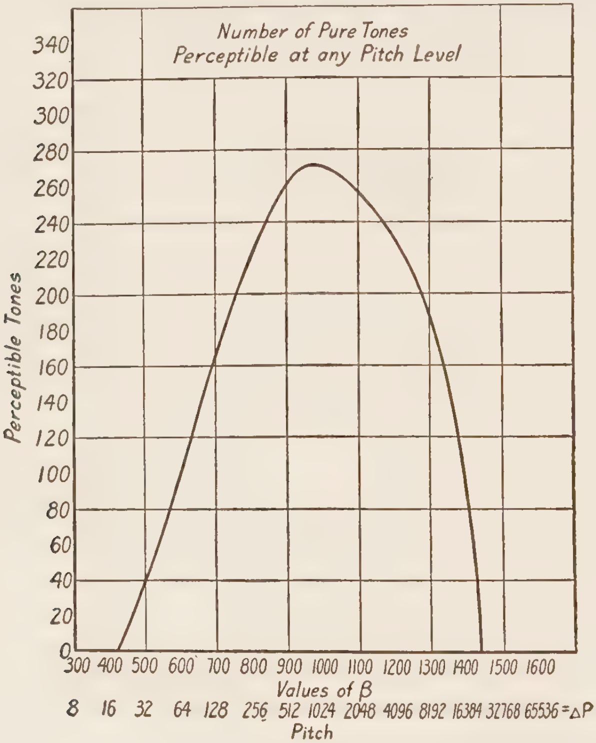


FIG. 68. LOUDNESS AS A FUNCTION OF ACOUSTIC FREQUENCY.

This curve shows the number of just-noticeably different loudness steps at all audible frequencies, when the pressure variation amplitude is kept constant at one dyne per square centimeter. This curve should be compared with the corresponding visual curve of Fig. 36. (*Fletcher: Bell System Technical Journal.*)

determine the absolute threshold as a function of the latter variable, assuming that the loudnesses of all tones are the same at this threshold condition. This study yields the lower curve shown in Fig. 67, which represents the pressure amplitudes required for liminal loudness over a wide range of frequencies. The upper curve of the figure shows the amplitude at which a tactual quality is added to that of tone, so that the area which is enclosed between the two curves may be taken to represent the domain of pure tonal sensation. A strictly psychophysiological formulation of the relation between loudness and wave-length must consist in a function which gives the number of just noticeable loudness steps from the absolute threshold up to the loudness which is realized at each frequency for a given constant energy (or amplitude, as desired). Although direct determinations of such functions appear not to have been made experimentally, Fletcher has computed representative curves having the required form. One of these is given in Fig. 68, for a constant pressure amplitude of one dyne per square centimeter. The position of the maximum, in this case, is at about a thousand cycles. The exact form of the curve depends upon whether pressure or amplitude are held constant and also upon the fixed intensity level which is selected. Wien [508] places the maximum of the audibility curve at 2200 cycles, for constant energy.

A study of Fig. 67 shows that the amount of pressure variation, which is required to evoke a just noticeably loud tone, varies tremendously with frequency. In the region of the minimum of the curve, 2000 to 4000 cycles, it is less than 0.001 dynes per square centimeter, which corresponds to a fractional change in atmospheric pressure of about one-millionth part, or a displacement of the air molecules by approximately one molecular diameter. These facts demonstrate the extreme absolute sensitivity of the ear in the specified frequency region. At about 20 and 20,000 cycles, approximately 3000 times as great a pressure variation is required. This corresponds to a factor of about 6,000,000 times in energy between 20 and 3000; and of about 6,000,000,000 between 3000 and 20,000 cycles, the difference between the two cases being due to the dependency of energy upon frequency, as well as upon amplitude. (Wien gives a factor of 100,000,000 between 50 and 2000 cycles.) In general, the low-frequency sounds which occur in nature or in music, tend to be of extremely high energy, compared with sounds having a higher frequency. This is a consequence of the relatively large mass and energy of the slowly vibrating objects. Hence, the natural low-frequency sounds may often yield great loudness, in spite of their low audibility; but the case is different for the extremely high frequencies, which are both relatively inaudible and usually deficient in energy, and hence seldom produce a high degree of loudness.

It is interesting to note that the wave-length for maximal audibility is approximately equal to the distance between the two ears (six inches), a fact which may have some bearing upon the principle of auditory localization by means of phase differences, which we have already discussed. (Volume I.) The exact form of the audibility curve shows variations from one individual to another, and in cases of deafness usually exhibits radical deviations in contour and a closing up of the area between the audibility and the tactile functions. The fractional diminution of the area in question can be taken as a measure of the deafness.[509]

342. Loudness as a Function of Intensity. — We may next consider how loudness varies as a function of the physical intensity of the stimulus, expressed either as energy or as pressure amplitude. In order to determine this function, a series of tones which are serially just noticeably different in loudness must be selected, and the energy values corresponding to them must be determined, the frequency being held constant. Fig. 69 shows the results of such measurements, the abscissae representing the logarithms of the energy, or power, and the ordinates the subjective loudness scale. It will be seen that the curve has the usual modified Fechner's law form, being a straight line above about 10^5, but flattening out considerably below this value. If we plot the relationship in the Weber form, we get the diagram shown in Fig. 70, which shows the relative threshold or Fechner fraction to be 1/10th, for the rectilinear portion of the Fechner relationship. This law is practically independent of frequency, and is closely similar in form to that

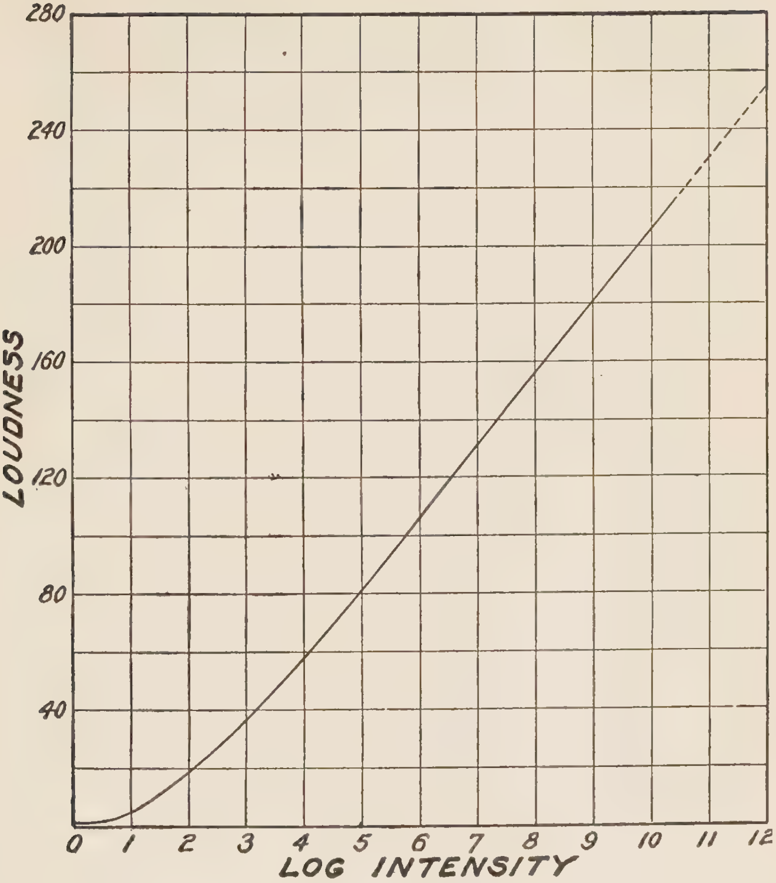


FIG. 69. LOUDNESS AS A FUNCTION OF ACOUSTIC INTENSITY.

This curve was obtained by graphical integration of the function represented in Fig. 70. The abscissae show the logarithms of stimulus energy, expressed in terms of the absolute threshold energy as a unit. This threshold, as shown in Fig. 67, differs radically for different frequencies, but the form of the curve is substantially independent of frequency, when plotted as in the present figure. The ordinates represent subjective loudness values, or the number of just-noticeable loudness steps from the absolute threshold. The degree of departure from the Fechnerian logarithmic relationship is evidently less serious than in the visual case. (*Cf.* Fig. 38.)

found by Nutting for brilliance. The Nutting equation, $\Delta I/I = P_m + (1 - P_m)\ (I_0/I)$ applies satisfactorily.[510]

343. Loudness as a Function of Frequency Composition. — Loudness can also be studied as a function of the composition of the stimulus in terms of different frequencies.[511] It has been found by Fletcher and his co-workers that in the case of two complex sounds which yield a noise of equal loudness, a proportional change in intensity may

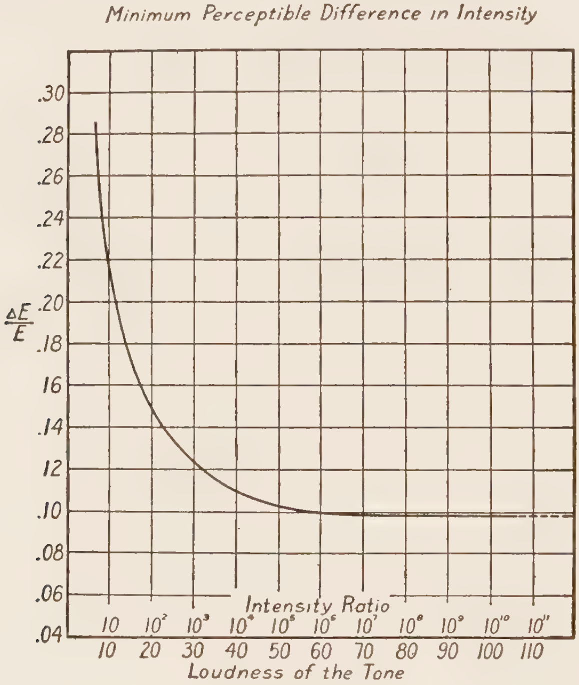


FIG. 70. ACOUSTIC INTENSITY THRESHOLD AS A FUNCTION OF INTENSITY.

The ordinates of this curve represent the smallest fractional change in the intensity of a pure frequency which is just perceptible at the intensity level determined by the abscissae. The abscissae are proportional to the logarithm of the stimulus energy, expressed in terms of the absolute threshold as a unit. It should be noted that the "loudness" values of the present figure, which is copied from the work of Fletcher, are of the arbitrary "acoustic" type (see Section 339) and hence are not to be identified with those of Fig. 69. (*Bell System Technical Journal.*)

disturb the equality. This phenomenon is analogous to the Purkinje phenomenon in vision. The exact relationship between the loudness of an auditory quality which is evoked by a harmonically complex stimulus, and the intensities of the individual harmonic components has not yet been determined for all cases.[512] The "masking effect," which we shall consider below, indicates that there is not necessarily an increase in loudness when one stimulus component is added to another. The result depends upon the exact relations of frequency and intensity between the components. In general, however, common experience shows that the loudness which attaches to a mixture of components is greater than that for any individual component.

Auditory Masking.—Very thorough studies have been made upon the effect of one frequency component upon the absolute loudness threshold for components having different frequencies. The phenomena which are observed in this type of experiment are classed under the heading of *auditory masking,* and are of the utmost importance for the developments of hypotheses concerning the mechanism of the auditory sense-organ. We shall therefore consider them in some detail.

It was stated by Mayer[513] that low frequency tones may completely obliterate those of higher frequency, but that the converse is not true. If a tuning fork of relatively high "pitch" is sounded while a low-frequency organ note is present, and the fork is allowed to run down until it becomes just inaudible, the removal of the organ note reveals the fork, still sounding at an astonishing level of loudness. Wegel and Lane[514] have made very accurate measurements upon this effect, and find that, in general, any two tones tend to mask each other, but that the action of low frequencies upon high ones is much greater than conversely. The effect decreases as the frequency difference increases, and increases with the intensity of the masking note. The law governing the action can be expressed by functions, or curves, which show how the threshold for the masked sound varies as a function of its frequency, for different frequencies and intensities of the masking sound. In each series of measurements, the latter is held constant, and the former

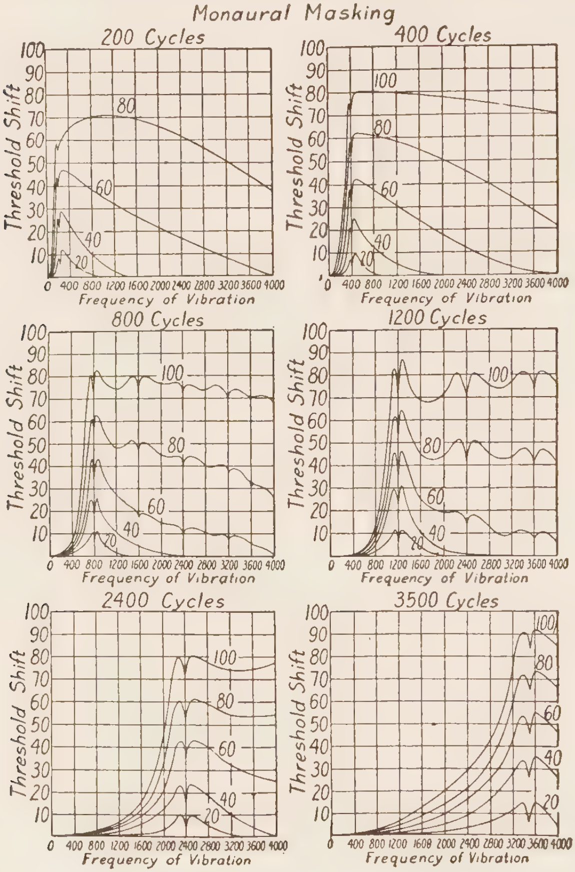


Fig. 71. Laws of Monaural Masking.

These curves show how the absolute intensity thresholds for acoustic frequencies, over a wide range, are affected by the presence of a constant, masking, frequency. The ordinates of the curve show the threshold change, while the various masking frequencies are specified above the corresponding graphs. This figure is reproduced from the work of Fletcher. (*Bell System Technical Journal.*)

is varied to determine the threshold at different frequencies. The curves shown in Fig. 71 exhibit the relationships in question for six separate masking frequencies at various intensities.

A study of these curves not only shows the general frequency directionality of the effect, as noted by Mayer, but also several other interesting features: (1) Increase in the intensity of the masking note greatly augments the masking on the higher-frequency side. (2) This high-frequency masking tends to show combined maxima and minima in the regions of even harmonics of the masking frequency. There is also a minimum or dip directly at the masking frequency, itself. Other phenomena which appear in this type of experiment will be discussed in the appropriate place, below. For the present, it is sufficient to notice how the conditions for threshold loudness, for one stimulus frequency, are affected by the presence of a stimulus having a different frequency. The effect upon loudness above the threshold has not been determined.

344. Pitch as a Function of Frequency. — Pitch is usually regarded as being indicative of the frequency of the sound stimulus, and its relationship to the latter seems to be more reliable than that of hue to frequency in the visual domain. In order to formulate this relation, we must set up a series of frequencies which yield serially just-noticeably-different pitches in consciousness, and then determine the identity of the frequencies in question. These frequencies will preferably be either of equal intensity or of equal loudness. Such an experiment has been performed by V. O. Knudsen,[515] who finds a law of the usual modified Fechnerian form. This is shown, for a representative loudness level in Fig. 72. From about 50 to about 500 cycles, the Fechner fraction shows a systematic decrease, but is constant from 500 to about 5000 cycles, above which it again increases. The subjective pitch scale can be regarded as being approximately a linear function of the frequency up to 500, while between 500 and 5000 it is a logarithmic function of the latter. The Weber type of relationship for the variables here concerned is plotted in Fig. 73. The just-noticeable fractional change (Fechner fraction) is 0.003 in the loga-

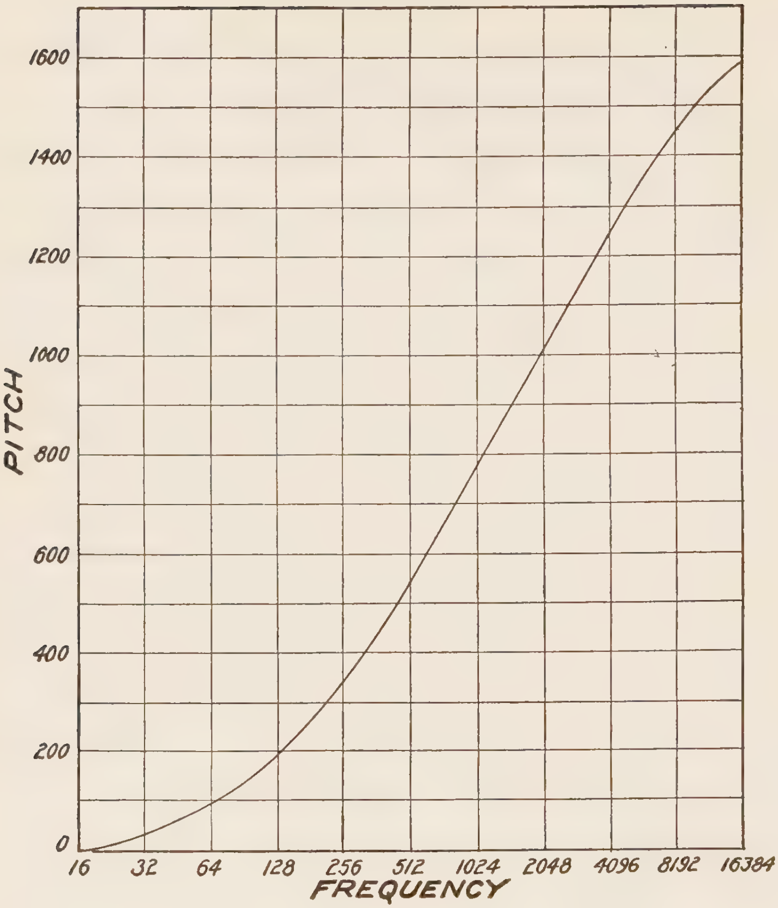


Fig. 72. Pitch as a Function of Acoustic Frequency.

This curve was developed quantitatively from the curve of Fig. 73, by graphical integration. The ordinates represent the psychological pitch scale number, or the number of just-noticeable pitch steps over the given frequency range. The abscissae are graphically proportional to the logarithm of the frequency, although the numbers show the frequencies directly. In integrating the function of Fig. 73, it was necessary to extrapolate extensively at the low frequency end, and the first threshold step was assumed to occur, with increasing frequency, at twenty cycles per second.

rithmic region; and amounts to about one cycle per second in the arithmetic region.[516] However, these "constants" are themselves functions of intensity or loudness. According to Knudsen, the Fechner fraction for frequency-pitch varies with intensity in about the same way as that which characterizes the Fechner fraction for intensity-loudness.

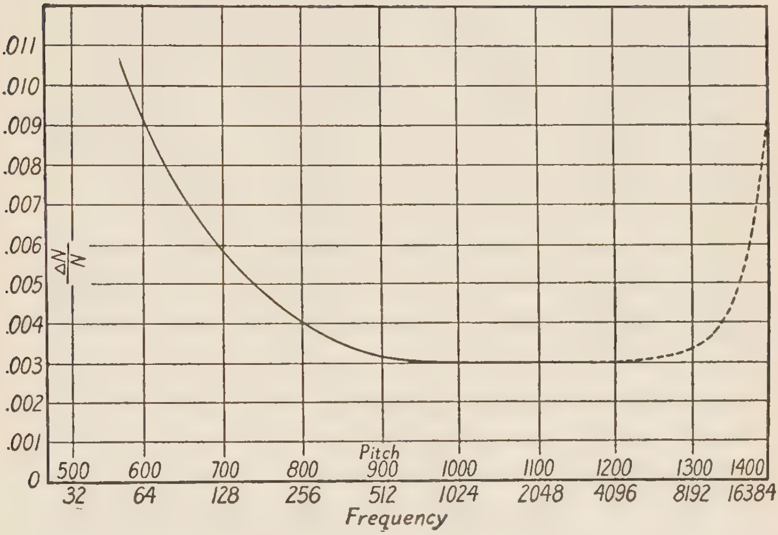


FIG. 73. RELATIVE ACOUSTIC FREQUENCY THRESHOLD AS A FUNCTION OF FREQUENCY.

The ordinates of this curve show the smallest fractional change in frequency which is perceptible at the frequency level determined by the abscissae. It will be noted that the curve has the form which is commonly found for intensity variations, with a substantially constant value of the relative threshold in a medium range of frequencies. It should be noted that the pitch values of this figure, which is copied from Fletcher's work, are arbitrary and not psychological, as in Fig. 72. (*Bell System Technical Journal.*)

The total number of just noticeably different pitches must obviously be a function of the intensity level of the stimulus, since the audibility limits approach each other continuously as the intensity is reduced. At a level of 10 dynes-per-square-centimeter amplitude, 1300 different pitches can be discriminated. Fletcher has computed the total number of pure tones which can be differentiated either as to loudness or pitch, within the area of pure auditory sensation of Fig. 67, and finds this number to be approximately 300,000, for the normal ear. It is found, experimentally, that very small changes in intensity and in frequency may produce the same, or an indistinguishable, effect in consciousness, indicating that the dimensions of loudness and pitch become confused within small regions of the pitch-loudness surface.[517]

345. **Pitch as a Function of Intensity.** — Certain considerations regarding the mechanism of the cochlea (*vide infra*) suggest that pitch, at a single frequency, should not remain constant, but should increase with an increase of the intensity of the stimulus. Psychophysical studies of this effect, if it actually exists, appear not to have been made. Changes in the subjective composition of the auditory experience, as a function of intensity, are well known and will be considered in the section dealing with compositional sensation.

346. **Pitch as a Function of Frequency Composition.** — When the tympanum is acted upon by a harmonically complex stimulus, the corresponding auditory experience tends to be similarly complex, being made up of a group of distinct pitches, each characterized by an appropriate loudness. This is the meaning of what is known as Ohm's law (for audition), which endows the auditory system as a whole with the properties of a harmonic analyzer. Apparently, therefore, pitch is independent of the frequency composition of the stimulus, because it is correlated solely with harmonic components, as such. However, as we shall see later, a number of different pitches may occur in conjunction with a single harmonic aspect of the stimulus, and when two or more stimulus components are present, the number of accompanying component pitches may be extremely large. In the first case, we have to deal with " subjective harmonics " and, in the second case, with " combinational tones," in addition to the harmonics. There is little doubt that all of these supernumerary pitches or tones are referable to actual

physical components, which are introduced by distortion in the response of the ear mechanism to the stimulus, so that, fundamentally, a one-one correspondence between harmonic components and constituent pitches may still obtain.

However, in spite of the analytical character of audition, it is still possible to speak of the pitch, or dominant pitch, of a tonal complex, such as a clang or a chord. When the complex is not analytically considered, it is judged as having a pitch and a timbre, and the former is determined as a rule by the lowest frequency in the combination. According to Farnsworth,[518] this is true only for the ordinary observer, while musically trained individuals tend to judge the pitch as corresponding to the highest component, because of their habit of recognizing the melody as being carried by the treble. Fletcher [519] finds that the pitch of a harmonically related combination of tones is that normal to the frequency given by the lowest and predominant *difference* between the several harmonic components. This frequency is identical with that of the fundamental in a normally produced clang, but the fundamental can be removed without altering the dominant pitch. The explanation of these facts lies in the re-production of the fundamental frequency by the summation of difference tones between its harmonics, in consequence of distortion within the ear itself. (*Cf.* page 246, below.)

347. Brightness and its Functional Relationships.— According to Rich,[520] brightness is the same function of frequency as is pitch, so that the two seem to act, in this relationship, like a single attribute. However, Ogden points out that the stimuli to vowel evocation yield variations in brightness that do not correlate with the corresponding pitch values, which are characteristics of specific vocality. Also, in the experiments of Abraham,[521] brightness was found to be diminished in the case of a sound given off by a siren, when the compression phase was shortened with respect to that of rarefaction, the frequency being constant. Hence it appears that brightness varies with frequency composition. It is also, in all probability, a function of intensity, increasing with loudness, while the pitch remains constant.

348. **Sensory Dependencies of Volume.** — Rich [522] has shown that volume is a logarithmic function of frequency,

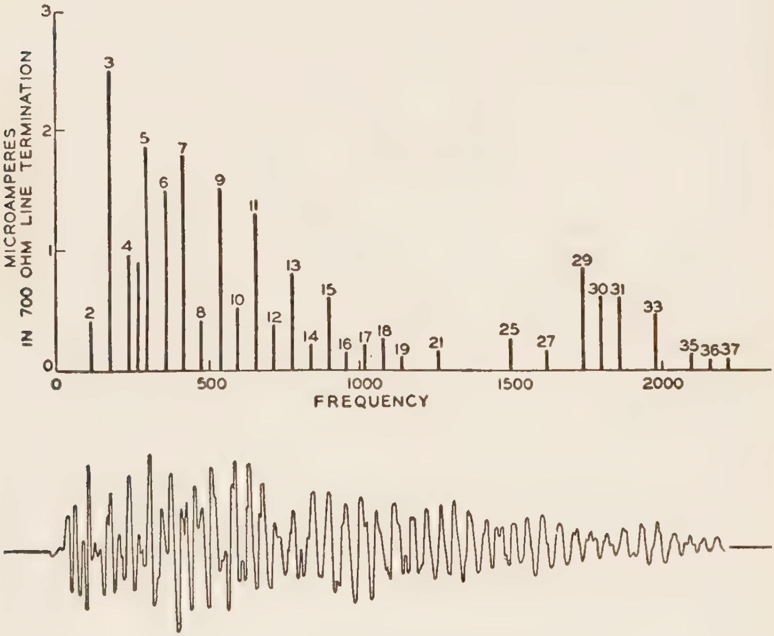


Fig. 74. Examples of Noise Stimuli.

The upper section of this figure shows a spectral analysis of noise received over a long distance telephone line, the intensity values being expressed in electrical units. The lower section of the figure represents the wave-form of the noise produced by the explosion of a sky-rocket. It will be noted that, although the vibrations, in this case, are aperiodic, there is a tendency for certain frequencies or wave-lengths to be predominant. The curve is copied from a photographic record made by Miller.

at least between values of 275 and 1100 cycles per second, the Fechner fraction being about 0.022, yielding 228 steps in all. The sensibility to volume differences is thus about one-tenth that to pitch differences, as compared on the frequency scale. Halverson [523] finds that volume increases with intensity, at a constant frequency.

349. Stimulus Relationships of Noise. — Our knowledge of the relations of noise experiences to their acoustic stimuli is less detailed than that of their specific dependencies upon mechanical events in the environment. In general, we can say that noises are related to temporal sequences of pressure change which resolve into a very complex and possibly infinite series of sinusoidal components. In a noise, these components are not uniformly related to one another harmonically, or in terms of integral numbers. Although such stimuli cannot ordinarily be analyzed by means of an harmonic analyzer, their pressure spectra can be determined by the use of appropriate electrical filter circuits. Fig. 74 shows the wave form produced by the explosion of a skyrocket, together with the spectrum of "line noise" on a telephone circuit. Some sounds, such as those which yield the "swishing" type of noise associated with office rooms, have a practically continuous spectrum.[524]

Noises are evoked, not only by analytically very complex continuative sounds, but by very brief acoustic impulses, even when the latter are fragments of pure harmonic waves. Such fragments, however, are also very complex from the standpoint of a Fourier's series analysis, since an incomplete sinusoidal vibration must be regarded as distorted, and as requiring components other than its fundamental for its mathematical reconstitution. When at least two cycles are given, a definite tone results, but mixed with noise, which decreases in proportion to the tonal component up to about sixteen cycles when the effect becomes almost purely tonal. In the case of the air disturbance which is produced by a siren, a noise results from a single puff, but a tonal element appears when two or more puffs are given.

Although noises may seem, in isolation, to lack the attribute of pitch, their comparison reveals differences in this dimension. It has been found that, in the case of noises which are due to very complex combinations of known frequencies, the pitch is approximately that corresponding to the average of all of the frequencies in the mixture. The loudness of noises is related to the total intensity of their stimuli by a law of the Fechnerian logarithmic type. Fischer and Wundt [525] found a relative threshold, or Fechner fraction, of .40 for noise, which is much higher than that for tones.

350. Sensory Correlations of the Vocables. — Although a careful subjective analysis may reveal some degree of complexity in certain of the so-called vocables, on the whole they appear as essentially unitary auditory experiences. A long series of physical investigations has been required to demonstrate the nature of the characteristic stimuli for these qualities. It will be recalled that, from the standpoint of the mechanism of their production by the vocal organs, the stimuli to the vocables are subdivided primarily into *voiced* sounds and *non-voiced* sounds. The former may be either continuative or cessational. The voiced sounds include the vowels, as continuative, and some of the consonants. The non-voiced sounds include such consonants as *p, t, ch, k, f, s, th* (thin), and *sh,* mostly fricatives or sibilants. The vowels can also be given a non-voiced form, as when they are whispered.

The main facts concerning the composition of the stimuli for the vowels are now fairly well established and confirm the theory of Helmholtz [526] that each vowel sound is characterized by a definite *region of resonance* in the frequency scale. It has long been recognized that each vowel has a specific tonality or pitch quality. Köhler [527] found the following relationships, through an introspective comparison of tones and vowels: $u = 260$, $o = 520$, $a = 1040$, $e = 2080$, $i = 4100$. However, since vowels can be sung at almost any desired fundamental pitch, they cannot be identified with pure tones. The facts appear to be that the stimuli to the vowels may have a complex and variable composition, but that each vowel sound is characterized by maxima of intensity in certain frequency regions, regardless of the identity of the fundamental. Thus, ā is produced when these resonant maxima are at or near 560 and 2000 cycles; ū at 475 and 4000; ō, at 600 and 3500; and ē, at 300 and 2500 cycles. Fig. 75 shows the distributions of intensity

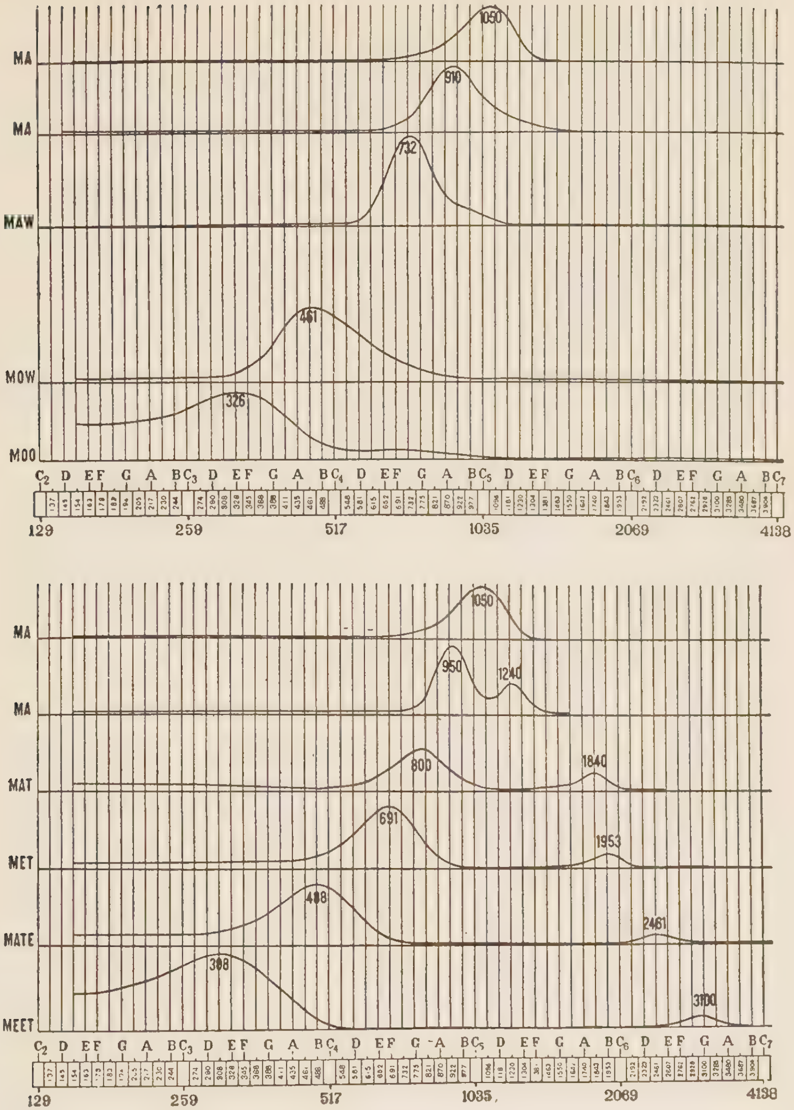


FIG. 75. ACOUSTIC ENERGY DISTRIBUTION IN CHARACTERISTIC VOWEL SOUNDS.

These curves show the distributions of energy found by Miller for the vowels indicated at the left of the figures. (*From The Science of Musical Sounds, Macmillan.*)

which D. C. Miller [528] found to be characteristic of certain vowels. It will be seen that one class of vowels has a single resonant region, while another class has two such regions in the frequency spectrum. These characteristic resonant maxima are known as the *formants* of the given vowel.

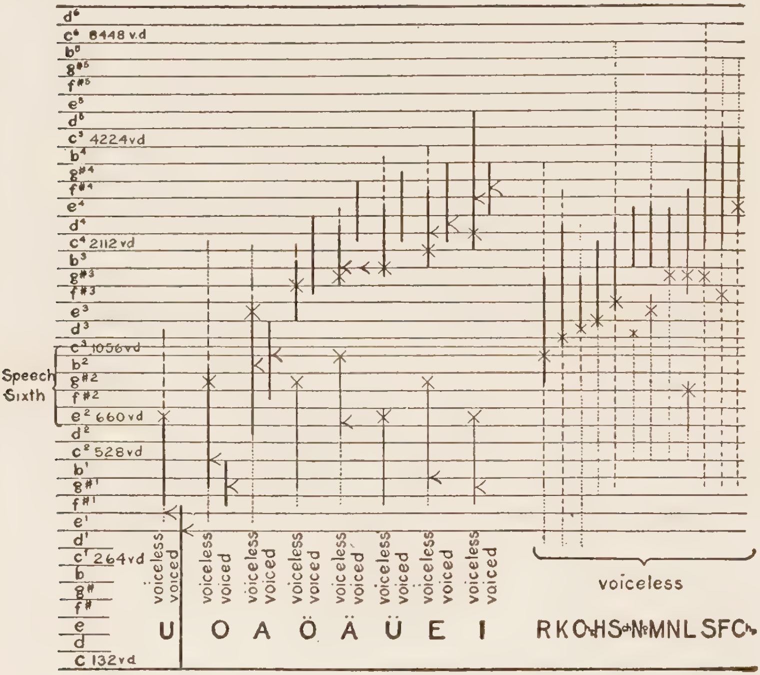


Fig. 76. Formants of Vowel and Consonant Sounds.

This diagram indicates the pitch or frequency positions of various vowels and consonants, both voiced and non-voiced. Heavy lines indicate the ranges of the primary formants and lighter lines the ranges of secondary formants. Less important ranges of resonance are designated by dashed and dotted lines, in order of importance. The arrow-heads show the positions of the vowel formants found by Miller. (*From Ogden: Hearing, Harcourt, Brace & Co.*)

The natures of the stimuli for the consonants have been established less definitely. The voiced consonants, or half-vowels, such as *m, n, l, r,* and *ng,* appear to have definite formants. Köhler finds that for *m* to be at 130 cycles. The fricative consonants are noisy but are characterized by the presence of relatively very high frequencies. Köhler's observers selected 8200, 17,000, and 34,000 for *s*, *f*, and *ch*, respectively. Stumpf[529] places the *m* formant higher and those for the fricatives lower, as shown in his diagram. (See Fig. 76.)

It has been suggested by Ogden[530] that the characteristic qualities of vowels, and possibly of other vocables, are associated with the *smooth* grouping together of a number of closely similar frequencies in distinct frequency regions. Thus, the vowel formants have a definite pitch, but are lacking in brightness because they have an energy distribution — without a sharp maximum — over a considerable frequency region, rather than a restriction of the intensity to a single frequency, as in the case of the pure tone which has the same pitch as the vowel formant. We shall come back to this point again in our discussion of the psychophysiological relationships of the cochlear mechanism and response.

Section 62

COMPOSITE AUDITORY SENSATION

Auditory experience shows two distinct forms of coexistential complexity. First, it has localization within auditory space. Secondly, certain auditory experiences manifest a definite internal constitution, in terms of distinct tone and noise components. As we have already noted, many forms of auditory consciousness apparently show varying degrees of *fusion*. Under conditions where we might expect to find distinct components, or an evident introspective complexity, there is merely a characteristic over-all quality. This is the case, for example, with the vowels and the vocables in general. It is also true, sometimes, as we shall see, that under conditions where we might expect the experience to be simple, or relatively so, it is actually very complex.

In our discussion of auditory perception, we have already considered the principal facts regarding auditory localization, and we have seen that, psychophysiologically, such localization rests upon the interrelations of stimuli at the two ears. We shall confine our attention, below, to the problem of the composition of the factors of auditory experience independently of their localization, and to the manner in which such composition is determined by monaural stimulus conditions.

351. Composition as a Function of Frequency and Intensity. — When the ear is stimulated by a single sinusoidal wave at low loudness, the resulting experience is a pure tone of definite pitch. However, if the intensity of the single frequency is raised, a second pure tone can ordinarily be distinguished, and it is found that this stands in the relation of a second harmonic to the original tone. In other words, it is a tone such as would accompany stimulation by means of a frequency double that of the one which is actually being used. Still further increase in the intensity of the pure harmonic stimulus yields a third harmonic tone, and even further increase, a fourth, and so on. It is clear that, under these conditions, if the primary frequency is varied, the tonal identity of the higher harmonics will change correspondingly, so that the composition of the experience is a function of both frequency and intensity.

352. Composition as a Function of Stimulus Complexity. — When the stimulus itself is harmonically complex, the composition of the corresponding experience will depend upon the other surrounding conditions. In the first place, the complexity of the stimulus must not exceed a certain critical value, or the stimulus will evoke a vocable or a noise. In the latter case, the corresponding experience will be simple, but qualitatively different from a tone or combination of tones. Secondly, the threshold conditions that are characteristic of the masking effect, which we have considered above, must be passed if the experience is to be complex even in the presence of a composite stimulus.

Now, if *two* pure sinusoidal frequencies are provided by the stimulus, and the higher of the two frequencies has sufficient intensity to overcome the masking effect, there will be two salient tones in consciousness, corresponding properly in pitch with the components of the stimulus. If three such stimulus components are present, there will be three corresponding experiential tones, and so on until the combination becomes excessively intricate. This separation of harmonic (or, perhaps, inharmonic) constituents by the psychophysical system is described by Ohm's law for audition, and seems to imply that the system in question has the properties of an harmonic analyzer.

Combinational Tones. — However, in the typical case, depending upon the exact intensity level and frequency relations of the stimulus constituents, we have a number of subjectively observable tones in addition to those which are represented in the stimulus. Neglecting any "subjective over-tones" of each principal component which may be present, we find a number of different classes of so-called *combinational tones.* Some of these tones have pitches corresponding to frequencies which are rather simple mathematical functions of the actually present stimulus frequencies.

Beats and Intermediate Tones. — Three different species of combinational tones have been recognized: the intermediate tones, the difference tones, and the summation tones. We may consider the psychophysical relationships of these tones for the simplest case, involving two pure frequency components, f_1 and f_2, in the stimulus. When these two frequencies are very close together, the resulting tonal experience is simple (except for possible subjective harmonics), although it may show the temporal phenomenon of *beats,* which we shall consider below. However, as the frequencies are gradually separated, a differentiation of pitch is finally apparent. Further separation, with a difference which depends upon the absolute magnitude of the frequencies in question, is accompanied by the appearance of a so-called *intermediate tone.* At first, this lies close to the lower of the two principal pitches and it is observed to carry the beats, the principal tones now being temporally steady. A further increase in the difference between the two frequencies is accompanied by a rapid increase in the pitch of the intermediate tone, so that finally it comes nearer in pitch to the upper than to the lower of the two principal tones. At a still higher frequency difference, it disappears entirely, after passing through a noisy phase.[531] The pitch of the intermediate appears not to be calculable in any simple way from the frequencies corresponding to the principal tones. This description of the behavior of the intermediate tone requires more extensive verification than has yet been accorded to it.

Difference Tones. — When the difference in frequency between the two stimulus components is in excess of about twenty cycles per second, a number of so-called *difference tones* may be heard. Their presence will depend upon appropriate absolute intensities and intensity relations of the two components in question. The first difference tone has a pitch corresponding to a frequency equal to $f_2 - f_1$, the difference between the principal frequencies. As a rule, this tone does not appear unless the difference is at least eighty cycles per second. Under certain conditions, due to the elevation of the threshold for the higher of the two principal tones or frequencies through masking, the difference tone may arise before the latter itself can be discriminated.[532] If the intensities of the two stimulus components are sufficient, a second difference tone will be present, and its pitch will correspond to a frequency equal to $2f_1 - f_2$. A third difference tone, of pitch corresponding to frequency, $3f_1 - 2f_2$, can also be recognized. This process continues, theoretically, *ad infinitum,* but the actual complexity of the consciousness is limited by the concrete intensities and frequencies of the given stimuli.

Summation Tones and the Total Complex. — Careful introspection will also reveal a *summation tone,* having a pitch which corresponds to the sum of the two frequencies, $f_1 + f_2$. Summation tones between the various difference tones, and between the difference tones and the principal tones, can also be detected. Thus Wegel and Lane [533] have identified the following components in the auditory experience due to two simple frequencies, 1200 and 700, respectively: f_1, 700; f_2, 1200; $f_1 + f_2$, 1900; $f_2 - f_1$, 500; $2f_2$, 2400; $2f_1$, 1400; $3f_2$, 3600; $3f_1$, 2100; $2f_2 + f_1$, 3100; $2f_2 - f_1$, 1700; $2f_1 + f_2$, 2600; $2f_1 - f_2$, 200 (?); $4f_1$, 2800; $2f_2 + 2f_1$, 3800; $2f_2 - 2f_1$, 1000; $3f_2 - f_1$, 4300; $3f_2 - f_1$, 2900; $3f_1 + f_2$, 3300; and $3f_1 - f_2$, 900. The exact frequencies were determined by the use of an exploring frequency which produced beats with the various subjective frequencies or tones. These values include the subjective harmonics as well as numerous difference and summation tones. Fig. 77 shows the distribution of some of these effects as functions of variable frequency and intensity of one of the principal sounds — designated as the "secondary tone" — for a fixed primary vibration. The figure necessarily discloses the masking effect, which limits all of these phenomena. Modern experiments upon the

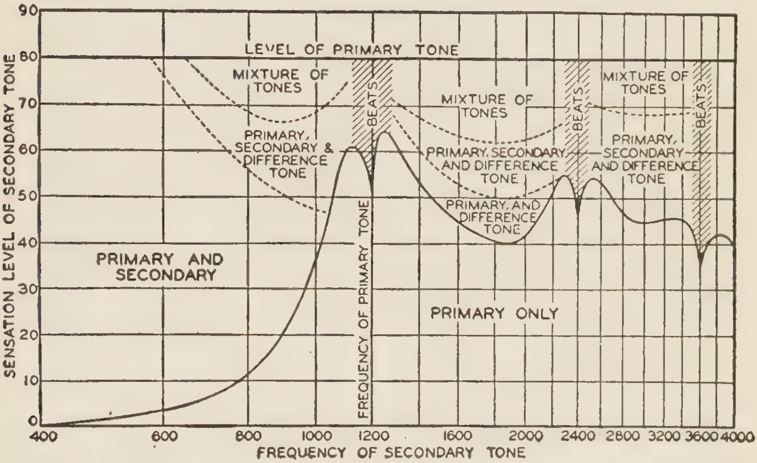


FIG. 77. SENSORY EFFECTS OF BITONAL STIMULI.

This diagram, from Fletcher's *Speech and Hearing*, represents the sensory accompaniments of a combination of two tones, when one of the two is constant and the other is variable in intensity and frequency. The former is designated as the "primary" and the latter as the "secondary" tone. See text for a more detailed explanation.

phenomena in question are made under conditions where it can be proven definitely that the combinational tones are not represented by any unintentional corresponding frequencies in the stimulus itself.

353. **Auditory Fusion.** — Introspective identification and report upon components of auditory experience, such as we have considered above, requires considerable training. However, the nature and basis of such training, or the possible changes in consciousness which may result from it, do not constitute a problem in sensation. These processes can best be considered in terms of the direct relationship of the experience to cerebral activities or conditions, but we should note here that the facts which we have expounded above relate primarily to the consciousness of a musically or introspectively trained individual. In the case of other persons, the various combinations of fundamental and over-tones, whether " subjective " or objective in their origin, are usually reported as qualitatively distinctive but unitary forms of experience.

Clangs. — A synthetic auditory quality of this sort, involving harmonically related frequencies or pitches, is known as a *clang*. As we have seen, clangs are ordinarily dominated by the fundamental pitch, the over-tones contributing to the so-called *timbre* or modulation of the fundamental tone quality. However, in some cases, this *dominant pitch* may correspond to a frequency which is not present at all in the stimulus, having the status merely of a difference tone. This effect occurs particularly in connection with groups of frequencies so related to one another as to constitute the principal harmonics of a low frequency note, which is itself practically or wholly absent. (*Cf.* page 223, above.) In this case, the auditory experience is that of a clang, dominated by the absent low frequency, which is represented subjectively by a difference tone. This difference tone may have a multiple causation, since all of the even harmonics differ from their neighbors by the amount of the fundamental frequency. Such a synthesis of low-frequency tones from their harmonics plays an important part in the improvement of effects obtained from modern electro-acoustic devices, which frequently fail to reproduce the fundamentals but render their actual harmonics satisfactorily.

Consonance and Dissonance. — Clangs are ordinarily associated with single vibrating bodies, like a piano string. When a number of strings are sounded simultaneously, we call the result a *chord.* Chords differ primarily from clangs in that their actual or potential tone components are more nearly equal in loudness. When a number of such similarly loud tones are presented simultaneously, their tendency to *fuse,* or to be replaced by a unified experience is a function of the mathematical relationships of the corresponding frequencies, even for the trained "musical ear." Thus, it has been noted that frequencies, one of which is double the other — or which stand in the octave relationship on the musical scale — "fuse" most readily. Frequencies having ratios of 2 : 3, 3 : 4, 4 : 5 also "fuse" more easily than do those having other frequency relationships, and in the order given. It appears [534] that the essential ratio numbers in tonal fusion are 2, 3, (4), 5, and possibly 7; 4 being a musical equivalent of 2. Departures from these ratios not only reduce the fusion, but introduce *dissonance,* a roughness or "beating" quality in the experience. It should be noted that the *consonant* frequencies stand in a relatively simple harmonic relationship to each other, just as do the frequency constituents of the stimuli to clangs, so that the conditions for the unification of the experience are probably the same in both cases. We shall consider so-called "explanations" of fusion in our discussion of the mechanism of the cochlea, below.

Section 63

TEMPORAL AUDITORY SENSATION

354. General Discussion of the Problem. — The normal stimulus to auditory experience is characterized by its temporal nature; sound frequencies obviously depend for their very existence upon *variations* of pressure as a function of time. However, introspection does not provide us with any evidence of this temporal change, in the characteristics of the component auditory experiences which we have considered in preceding sections. It is, of course, true that all of these experience factors *endure,* and that none of them can be generated or destroyed instantaneously. Nevertheless, they are by definition without structure in introspective time, and can therefore be conceived as capable of instantaneous existence without loss of character. Experiments, similar to those of Abraham, with temporally truncated tonal stimuli, provide us with no evidence whatsoever as to the temporal constitution of the corresponding auditory experiences. It is quite evident that temporal complexity in the stimulus is translated into non-temporal quality in experience.

However, auditory experience is, *par excellence,* a field for very significant temporal variation, so that we need to consider some of the relationships which exist between such changes and the corresponding stimulus conditions. The temporal patterns of noises furnish one of their most important features, from the standpoint of their intellectual or emotional meaning. Speech obviously depends for its utility as a means of intercommunication upon the temporal sequence of different sounds; and music is also a pattern in time. In general, we can say that alterations of any stimulus characteristic, in time, will be followed by corresponding changes in experience, the laws of this correspondence being determined by the psychophysical relationships which we have considered in detail above. If the frequency is altered, the pitch and loudness will follow in accordance with their established dependencies upon frequency. If the intensity or the composition varies, there will be an accompanying alteration of loudness or timbre, and so on. Thus, the psychophysical laws which we have already presented provide a lexicon for translating the temporal pattern of the stimulus into that of the related experience.

However, there will undoubtedly be some features of the experience which will not be accounted for in such a translation, and which are due to transitional influences, or the necessity of representing the experience as a function of the time aspect of the stimulus. It is certain, in the first place, that there will be a *lag* between any stimulus change and the corresponding experimental modification. If we adhere to our fundamental assumption that the cortical process and the auditory consciousness are simultaneous, this lag must be attributed to the time required for the change to be propagated to the sense-organ, to modify the processes of the latter, and to be transmitted along the auditory nerves to the brain. It is furthermore to be supposed that the exact function, which represents the stimulus change in time, will not be accurately reproduced by the temporal course of the corresponding feature of the auditory experience. For example, a practically instantaneous alteration in the stimulus intensity will presumably be followed in experience by a relatively gradual, although rapid, transition. Theoretically, we can study each of the auditory attributes as a function of time after a change in any characteristic of the stimulus. The difficulties of making such studies experimentally are somewhat greater than in the case of vision, but are not insurmountable in any case.

355. Critical Interruption Frequencies for Tones. — In general, we can say that the temporal or transitional effects in audition are less marked than in vision, and in the majority of other senses. The auditory sense shows a low inertia in following changes in the stimulus, a minimum of after-effects, and is comparatively indefatigable. Mayer [535] found that interruptions at the rate of 27 per second for a 64 cycle frequency and at 204 per second for a 1024 cycle frequency gave just appreciable breaks in the corresponding tones. Allen and Weinberg [536] have determined the minimum rate of interruption of tones of various frequencies, at which a smooth tone impression can still be secured, and find that it is inversely proportional to the square-root of the logarithm of the pressure amplitude, and directly proportional to the square-root of the logarithm of the acoustic frequency. This means that the persistence of audition increases with intensity and decreases with acoustic frequency. The general order of magnitude of the critical interruption frequencies, in terms of acoustic cycles, agrees with the results of Mayer: three or four of the latter per interruption. However, Kucharski [537] finds that 500 interruptions per second in a 1000 cycle tone yields an appreciable unevenness while with 100 interruptions in a 200 cycle note clear discontinuities are recognized by all observers. In general, we should expect the time of rise or decay of the tone to be not less than about two complete cycles of the given frequency, since experiment shows that a single isolated cycle does not suffice to yield a tonal effect.

356. After-Effects and Adaptation. — Urbantschisch [538] has noted primary after-tones, lasting from one to ten seconds subsequently to the cessation of the stimulus. He has also demonstrated recurrent after-tones appearing for one or two minutes at irregular intervals and lasting ten to fifteen seconds. Ordinarily, they are of approximately the same pitch as the original but of reduced loudness. Intense memory images of tones are experienced by some people hours after the original stimulus exposure, particularly when the latter has been quite lengthy. Pattie [539] has shown that a noticeable decrease in loudness results from protracted stimulation of one ear with a single frequency, and that this condition may last as long as thirty seconds. It is not specific to the fatiguing frequency but affects all reacting frequencies in the same manner. Pattie's method involves the fact that the adaptation is at least partially specific to the ear which is subject to the fatiguing stimulus.

357. Auditory Beats. — One of the simplest temporal phenomena of auditory sensation is that of *beats*. We have already discussed the physical basis of this effect, in the fact that when two different sound frequencies are operative in the same medium, such as the air of the external auditory canal, they alternatively weaken and reinforce each other with a periodicity which is equal to the arithmetical difference between their vibration rates. This action is not limited physically to frequencies which are closely similar, but applies to all frequency combinations whatsoever. If the beat-frequency is not too rapid, it is represented in experience by a periodic fluctuation in loudness: a sort of auditory flicker. This can be recognized introspectively as a temporal process of the loudness attribute, although it has a variable qualitative character of its own. We have already noted that the beating is sometimes carried subjectively by a tone which lies intermediate between the tones corresponding to the two interfering frequencies in the stimulus.

According to Titchener,[540] as the frequency of the beats increases, "they grow harder and less billowy, so that they may be compared to the rattle of a kettle-drum, or even to a rapid succession of hammer-strokes upon an anvil. As the pitch-numbers diverge still further, the separate beats give place to an unanalyzable roughness, harshness or hoarseness, which with yet wider separation of the generators finally disappears." The lower threshold for the recognition of beats appears to be about one beat per 180 seconds, and the higher threshold, twenty to thirty per second, at which point, however, they are becoming harsh. This harshness enters at a beat-frequency that is lower the higher the two frequencies which are interfering.

Beats can also be evoked in experience under conditions where there is no corresponding beat-periodicity in the stimulus. Such "subjective beats" occur when a relatively weak "exploring" tone approaches the pitches of subjective harmonic, difference, or summation tones. In other words, these supernumerary tones behave in relation to an externally present frequency as if they were contained in the stimulus, although, in fact, they are absent. As a rule, the frequency locations of these supernumerary tones can be determined far more accurately by means of their beats, with an exploring tone, than in any other manner. The exploring tone will develop beats in the neighborhood of such subjective harmonic, difference or summation tones when the latter, *per se*, are not introspectively reportable.

358. Music and Speech. — Music and speech are, of course, determined in their temporal patterns by the exact sequence of stimulus frequencies, intensities, and frequency compositions. Hence, they must be regarded as having a definite correlation, in the time dimension, with the temporal pattern of the stimulus, and to this extent as possessing a sensory psychophysiology. However, the outstanding features of these experiences must receive their physiological explanation primarily in terms of cerebral, rather than sensory, factors. We are here referring to their meaningfulness, aesthetic quality, relation to emotion, etc. The exact successions of qualitative components which they comprise are already explicable on the basis of the facts and principles which have already been presented above.

Section 64

PSYCHOPHYSIOLOGICAL RELATIONSHIPS OF THE AUDITORY SENSE-ORGAN

The next step in our study must be to trace the response propagation, along its path from the sound vibrations within the external auditory meatus through the various successive links of the auditory sense-organ. Now, the latter is physically very complex, consisting of an intricate series of component mechanisms, and hence of response sub-stages. It will not be profitable to consider each one of these parts in isolation from the others, and hence we shall deal with the entire sense-organ stage or process as a unit. This process may be defined as beginning with the response of the tympanum, and as ending with the excitation of the auditory nerve fibres. As in the case of vision, there are certain methodological principles which we should bear in mind: (1) that our reliable knowledge concerning the sense-organ processes is relatively slight, so that we are forced to have recourse to hypothesis, (2) that the psychophysical relationships which we have already established between the stimulus and experience, may provide us with very important data for determining the best hypothesis, and (3) that such an hypothesis should bring about a simplification of psychophysiological principles, as these are reformulated for the sense-organ stage.

359. The Structure and General Dynamics of the Ear. — The general anatomical structure of the ear mechanism

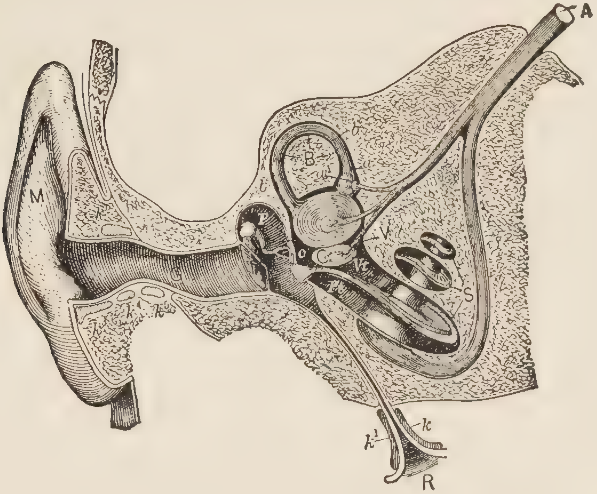
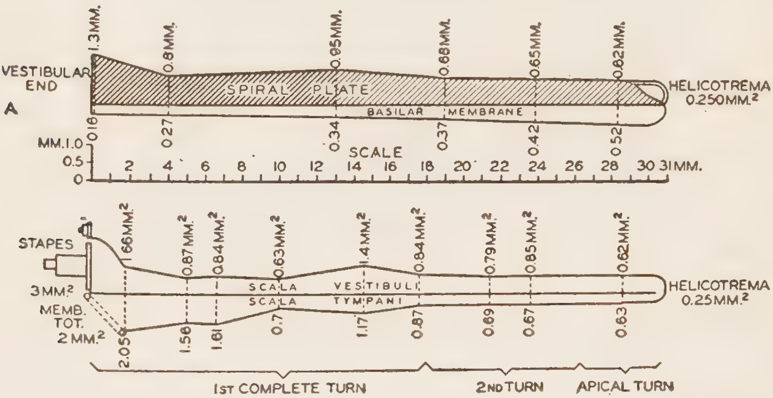


FIG. 78. THE MECHANISM OF THE HUMAN EAR.

This is a schematic section of the ear, with the parts of the inner ear much enlarged for clearness. *M* and *G* constitute the external ear. The middle ear, with its ossicles, is shown at *P*. The inner ear includes the cochlea, *S*, and the semicircular canals, *B*, with their attached parts. The auditory nerve is shown at *A*. The natural position of the cochlea would cause its apex to face the observer, so it has been turned through an angle of ninety degrees in order to reveal its structure. (*From Pillsbury: Fundamentals of Psychology; Macmillan.*)

is shown, in conventionalized form, in Fig. 78. The tympanum is bowed inwards, and is so composed of radial and circular fibres, in web formation, as to make it substantially aperiodic or of very high natural period. Its movements, in response to the pressure variations which constitute stimulus, are transmitted to the ossicles (or ear-bones) in the middle ear space, which is filled with air. These bones form a lever of the second order type, having a ratio of 3:2, the axis of the lever being horizontal and at the edge of the tympanum, somewhat suggesting the construction of a mechanical phonograph reproducer unit. The vibrations are thus transmitted to the oval window (*fenestra ovalis*), with an increase of pressure and decrease of amplitude, the maximal movement of the stapes probably being not greater than 0.04 millimeters.

The oval window is covered by a membrane which has about 1/20th the area of the tympanum, so that the total increase in the pressure is by a factor of 30. The vibrations are passed through the membrane to the endolymph of the scala vestibuli, which is shown (together with other portions of the apparatus) in uncoiled form in Fig. 79. Within the scala vestibuli, the pressures can be released in two different ways: (1) by a bodily movement of the liquid along the whole length of the scala, through the so-called helicotrema, or opening communicating with the scala tympani, and thence along the latter to the round window, which is also covered by a flexible membrane, or (2) through displace-



1.3MM.
0.8MM.
0.95MM.
0.68MM.
0.65MM.
0.62MM.
VESTIBULAR END
A
SPIRAL PLATE
BASILAR MEMBRANE
HELICOTREMA 0.250MM.²
.016
0.27
0.34
0.37
0.42
0.52
MM. 1.0
0.5
0
SCALE
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 31MM.
1.66MM.²
0.87MM.²
0.84MM.²
0.63MM.²
1.4MM.²
0.84MM.²
0.79MM.²
0.85MM.²
0.62MM.²
STAPES
3MM.²
MEMB. TOT. 2MM.²
SCALA VESTIBULI
SCALA TYMPANI
HELICOTREMA 0.25MM.²
2.05
1.58
1.61
0.7
1.17
0.87
0.89
0.67
0.63
1st COMPLETE TURN
2nd TURN
APICAL TURN

Fig. 79. Dimensions of the Basilar Membrane and Associated Parts.

In this diagram, due to Fletcher, the basilary membrane, the spiral plate, and the scalae vestibuli and tympani are represented as uncoiled so as to permit their actual dimensions to be shown. (From *Speech and Hearing*.)

ment of the basilar membrane, which forms the partition between the two scalæ. The actual result is a compromise between these two tendencies, the quantitative balance being a function of the sound frequency. The total length of the basilar membrane in the human being is about 32 millimeters.

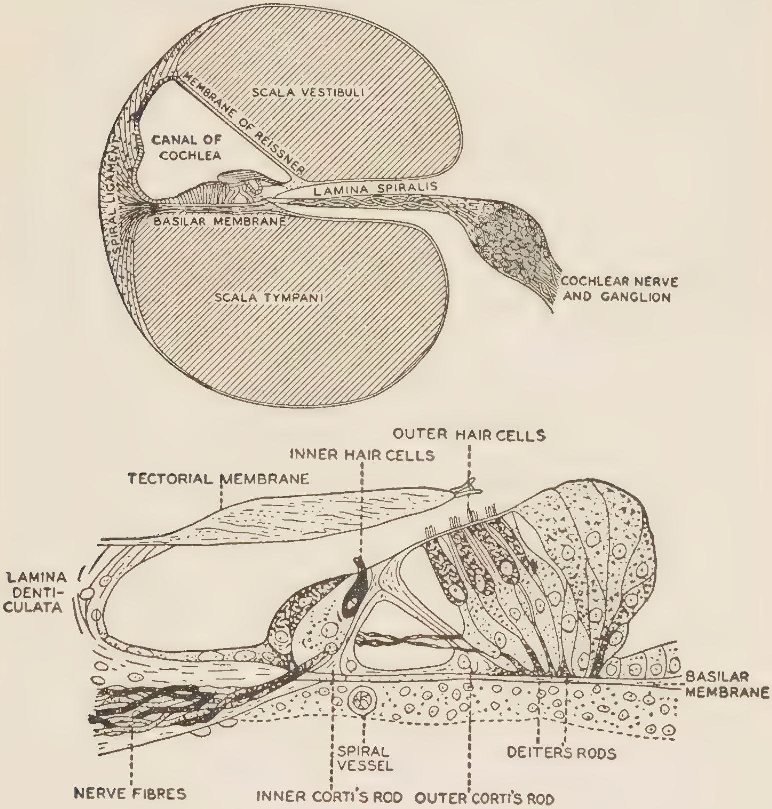

SPIRAL LIGAMENT
MEMBRANE OF REISSNER
SCALA VESTIBULI
CANAL OF COCHLEA
LAMINA SPIRALIS
BASILAR MEMBRANE
COCHLEAR NERVE AND GANGLION
SCALA TYMPANI
OUTER HAIR CELLS
INNER HAIR CELLS
TECTORIAL MEMBRANE
LAMINA DENTICULATA
BASILAR MEMBRANE
SPIRAL VESSEL
DEITER'S RODS
NERVE FIBRES
INNER CORTI'S ROD
OUTER CORTI'S ROD

Fig. 80. Transverse Sections of the Human Cochlea and Organ of Corti.

The upper diagram in this figure shows a typical cross-section of the cochlea. The structure mounted upon the basilar membrane is the organ of Corti, which is shown in greater detail in the lower diagram. (*From Fletcher: Speech and Hearing.*)

Mounted upon this latter membrane, is the so-called *organ of Corti,* which supports the receptor cells. (See Fig.

80.) No functional interpretation is required of the exact structure of this organ, but the general arrangement is such that a movement of the membrane applies stresses to the hairs of the receptor cells and presumably stimulates the latter mechanically. According to McKendrick,[541] 14,000 separate conducting fibres of the eighth cranial nerve are distributed about evenly along the length of the membrane, from the oval window to the helicotrema. There are two lines of hair-cells, the inner line containing about 3500 and the outer approximately 12,000 cells, making a total of 15,500, so that there is about one auditory fibre for each cell. It is undoubtedly correct to assume that the auditory receptors have a definite threshold, in terms of amplitude of vibration of the membrane, which must be exceeded before they will arouse a nerve impulse. The simplest view regarding the process of stimulation, would be that a single impulse is generated for each complete vibration cycle, and that each section of the basilar membrane actuates its own nerve fibre independently of the actuation by other sections.

360. Theories of the Basilary Response. — A great many highly speculative hypotheses have been advanced concerning the manner of response of this cochlear apparatus, and regarding the relationship of various aspects of its process to auditory experience. We may mention the following typical theories: (1) Helmholtz's resonator theory,[542] according to which the basilar membrane consists of a large number of fibres which are individually resonant so as to cover the entire gamut of audible frequencies, (2) the "telephone" theories of Rutherford,[543] Voltalini,[544] Waller,[545] and others, according to which the entire membrane vibrates as a whole in synchronism with all frequencies, and (3) the pressure-pattern theories of Ewald,[546] Meyer,[547] ter Kuile,[548] Gray,[549] and others, according to which there is a variation in the amplitude of the response of the membrane, from one point in its length to another, depending upon principles other than resonance. However, the investigations of Wegel and Lane,[550] and their associates, provide us with an analysis which approximates the ideal of a really scientific demonstration of the mechanism, and leads to a view which is much more satisfactory than those previously advanced. It incorporates some of the features of the earlier hypotheses, but places them upon a substantial theoretical and experimental foundation.

Since the ear mechanism is subject to known mechanical principles, it should be possible to determine its manner of response, up to the point of nerve stimulation, from a knowledge of its exact structure. Unfortunately, however, the various mechanical constants which are involved have not been very accurately ascertained, so that a strict dynamical analysis is not yet feasible. Nevertheless, a semi-quantitative line of reasoning permits us to become fairly certain regarding the main features of the process. Telephone engineers find it convenient to replace the mechanical aspects of the system by equivalent electromagnetic features, thus setting up a complex network of conductors, or a "filter," which shows properties analogous to those of the mechanical system of the auditory mechanism. This method of treatment points the moral that we should try to understand the action of the ear not in terms of any isolated part, such as the basilar membrane, but as the coördinated response of a large number of closely coupled components.

361. The Dynamics of the Inner Ear. — Let us suppose a sound — of variable frequency, intensity, or frequency composition — to be acting upon the tympanum, and let us see what presumably happens when we vary its characteristics. Starting, first, with frequency: at very low frequencies (perhaps less than twenty cycles per second) the motion is effectively transmitted to the fluid of the inner ear, but the changes in pressure are so slow that there is plenty of time for the liquid to move back and forth through the helicotrema, and hence the displacement of the basilar membrane is insufficient to excite any of the nerve fibres or hair cells. As the frequency is increased, the mass of the fluid will resist the vibratory forces, more and more, so that the membrane will be subjected to an increasing oscillatory displacement. Mathematical analysis, as well as experience with analogous filter networks, shows that this displacement should first appear near the helicotrema, progressing towards the oval window as the frequency increases. At very high frequencies, there will be substantially no longitudinal motion of the liquid, the entire disturbance being transferred across the membrane, very close to the oval window. Thus, although the basilar membrane will tend to move in its entirety for any frequency, it will show a maximal amplitude at a point along its length which is definitely localized as a function of the frequency in question. At extremely high frequencies, say above 30,000, the total mass of the transmission system, including the ossicles, may be so great that practically no vibration is imparted to the basilar apparatus.

In the case of a stimulus which involves more than one pure sinusoidal vibration, we should expect to find a pattern of vibrations upon the membrane, such as would be obtained by a superposition of the patterns which are characteristic of the individual components by themselves. If the intensity is low, there will presumably be the same number of maxima as there are sinusoidal components in the stimulus. However, if the intensity is high, this condition cannot be guaranteed, for the reason that a mechanism, such as that which we have described, inevitably introduces the effects of so-called non-linear distortion. These are attributable to the fact that the displacement of various parts of the apparatus does not follow Hooke's law, or is not at all times proportional to the acoustic pressure. It operates after the fashion of an overloaded vacuum tube amplifier, or the " detector " in a radio set, emphasizing the inward movements as compared with the outward movements, or *vice versa.*

It can be shown mathematically, as well as by experiments with vacuum tubes, that this form of distortion will introduce the following types of adventitious vibration: (1) a series of harmonics of any given frequency, which will increase in amplitude relative to that of the fundamental, as the intensity increases, (2) when two or more frequencies are applied, a complex assembly of difference frequencies, and (3) under the same conditions, summation frequencies of various orders. The necessity of these conclusions is beyond dispute from the physical standpoint. Consequently, we should expect the pattern of vibration of the basilar membrane, at relatively high levels of excitation, to be much more complex than that which accompanies very low intensities, for the given frequency composition of the stimulus.

362. Basilary Relations of Pitch and Loudness. — We are now in a position to make certain deductions regarding the psychophysiological relations of the inner ear process. These deductions are based upon established relations between the stimulus and experience, on the one hand, and between the stimulus and the sense-organ process, on the other hand. The combination of these two sets of data should enable us to ascertain some of the relationships between the experiential factors and the various aspects of the sense-organ process.

We may consider, first, the status of pitch and loudness for a single sinusoidal stimulus, under conditions of relatively low intensity or, perhaps better, of low acoustic loudness. It will be evident from the foregoing discussion that the exact frequency of the stimulus is transmitted unchanged through the entire ear system, so that this same vibration rate is imparted to the basilar membrane, and the receptor cells will be subjected to a series of impacts at the rate in question. Simultaneously, the frequency receives a second representation in terms of the position of maximal amplitude of displacement of the membrane, this position being near the helicotrema for low frequencies and near the oval window for high. Hence, pitch is correlated with (1) the frequency of irritation of the hair cells, and (2) the identity of the cells which are maximally affected. Where the intensity of the action exceeds the absolute threshold, we must suppose that a band of hair cells is simultaneously excited. In this case, the excitations will all be at the same frequency, in synchronism, and the position of the band may be considered as determined either by its extremes or by its middle point.

The intensity of the stimulus, for any single frequency, will have a triple representation, firstly, by the average or maximal amplitude of the basilar displacements, secondly, by the width of the band of supraliminally excited receptors, and thirdly, by the ratios of the amplitudes of the distortion harmonics to that of the fundamental. However, when the frequency is varied, these factors will not remain similar if the amplitude of the stimulus is held constant, on account of the changes in efficiency of transmission of the sound from the tympanum to the basilar membrane. Such similarity might be maintained, at least approximately, if a series of stimuli of equal acoustic loudness were employed. Now, loudness cannot be correlated exclusively with the proportion between the harmonics and the fundamental, since loudness varies with intensity when the harmonics are subliminal. Furthermore, the statement of such a proportion seems to imply a prior representation of loudness or its neurological equivalent, each harmonic having its own private loudness value. Hence, it appears that we must relate loudness to (1) the amplitude of the basilar displacements, or (2) the number of supraliminally excited receptors, or both.

363. Basilary Relations of Brightness and Volume. — The relationships of brightness and of volume present greater deductional difficulties. *Brightness* is the same function of fequency as is pitch, but varies with the manner of distribution of intensity among a number of adjacent frequencies. If we follow the ideas of Ogden [551] (and also of D. C. Miller), we shall be led to believe that a pattern of excitation of the basilar membrane having a sharp maximum yields a brightness superior to that which accompanies a blunter distribution, in the same pitch region. This notion would lead us to look for sharper maxima at high than at low frequencies for the same loudness (or some other appropriate standard condition). That this is the case is suggested by some of the studies of Wegel and Lane,[552] and by the general principles which determine resonant response. The sharpness or bluntness of the distribution can be conceived to be represented by a corresponding distribution of excitation intensities among the receptor cells.

Volume must be correlated with some feature of the basilary response which can be interpreted as increasing as frequency decreases, and also as increasing with intensity or loudness. Anatomically, the width of the membrane is greater in the region which is affected most strongly by low-frequency vibrations, and it is possible that the distribution of the disturbance across the membrane width increases with the magnitude of the displacement. It will be recalled that there are two parallel lines of hair cells on the membrane, so that it would not be impossible for such a factor to receive representation in the nerve impulse. However, a more plausible idea will appear when we come to consider the probable relationships of the nerve impulses themselves to the auditory attributes in experience.

364. The Resolution of the Laws Governing Loudness. — The correlations which have been indicated above, are sufficiently definite to permit us to effect an appreciable simplification of the psychophysiological relationships for the basilary, as opposed to the stimulus, stage of the response, at any rate for the case of pure tones or their harmonic combinations. The *audibility curve,* or the manner in which loudness varies as a function of frequency, is evidently explicable — at least in part — by the variation in the efficiency of acoustic transmission between the tympanum and the basilar membrane. The mechanism, as described, is evidently such as to lead to a single maximum of this efficiency with radical falling-off, practically to zero, at very high and at very low frequencies. Hence, it is conceivable that loudness is directly proportional to the number of fibres which is excited at any given frequency, or to some other simple combination of factors pertaining to the inner ear mechanism. In this case, the audibility curve is primarily characteristic of the stimulus-basilary relationship, and not of the relationship between the receptor excitations and consciousness.

It is highly probable that the same proposition is true of the law which associates intensity with loudness, for any frequency. Our conclusion here must depend, however, upon whether we choose average amplitude or width of band as the essential feature. In the latter case, the relationship should be of a semi-logarithmic form, if we suppose the distribution to follow the usual laws of resonance. This very fact may appear to be a reason for choosing width, rather than amplitude, as the crucial correlate of loudness.

The *masking effect* is also evidently interpretable in terms of a stimulus-basilary relationship. Following the ideas of Wegel and Lane, we may suppose that the masking frequency excites a portion of the membrane, along its length, which increases with intensity; and at high intensities the distortion harmonics introduce bands of excitation at double, triple, etc., the primary frequency. In order that a secondary, or exploring, frequency should become audible, it must bring about an appreciable change in the excitation in its own locality. The conditions for such a threshold effect can be conceived in several different ways. According to Wegel and Lane we have to do with a just noticeable increase in amplitude, as such. However, it seems more likely that the exploring tone must excite hair cells which are not already being excited by the primary frequency. The asymmetry of the masking effect, on the frequency scale, is attributable to the existence of the distortion harmonics, which involve bands of the membrane above, but never below, that for the primary frequency. That masking is due solely to a feature of the sense-organ process is shown by its absence when the primary and secondary frequencies are applied (say) to the right and left ears, respectively. In this case, the masking action is about one percent of the monaural value,[553] which corresponds to the probable magnitude of the "bone conduction" from one side of the head to the other.

365. The Resolution of the Laws for Pitch. — The exact manner in which pitch, measured on a liminal scale, varies with frequency is not represented in any of our ideas concerning the relationship between the stimulus and the action of the basilar membrane. However, Wegel and

Lane have employed this stimulus-experience relationship to provide a basis for plotting out the loci of various frequency maxima upon the membrane, arriving at the result shown in Fig. 81. They assume that just-noticeable pitch differences are represented by equal linear distances on the membrane. On this basis, a single threshold corresponds to 0.02 millimeters. Their scheme is evidently based upon the assumption that pitch is determined by the position of maximal response, rather than by the actual frequency of basilary vibration, an assumption which is somewhat questionable, as we shall see below. On account of the non-linearity of the response of the ear, the exact positions of the maxima should change with intensity, yielding a variation in pitch, an effect which has not been demonstrated experimentally.

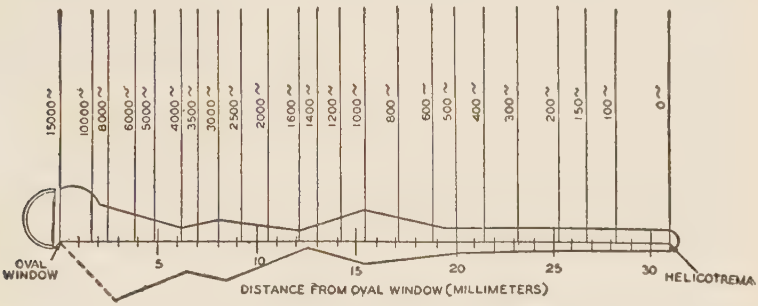


Fig. 81. Distribution of Acoustic Frequencies along the Basilar Membrane.

This diagram shows the points of maximal response of the basilar membrane, according to the hypotheses of Wegel and Lane. (*From Fletcher: Speech and Hearing.*)

The facts which are expressed in *Ohm's law* for audition can be correlated with the separate localization of distinct frequencies on separate bands along the length of the basilar membrane. So long as these bands do not appreciably overlap, there is an actual spatial separation of the component frequencies, and hence analysis in the truest sense. From the standpoint of pure kinematics, such separation is never complete, but since the hair cells must have a definite threshold of excitation, the separation may actually be perfect under appropriate conditions as tested by the receptor response.

It is evident that the phenomena of *subjective harmonics, difference, and summation tones* can be attributed to the presence of actual vibrations on the basilar membrane at the indicated frequencies. These supernumerary frequencies are introduced by the non-linear distortion of the ear mechanism, and are indistinguishable, within the ear, from objectively present components. Consequently, it is highly probable that all corresponding relationships can be eliminated as between the basilary vibrations and consciousness. The production of beats between an exploring stimulus frequency and these distortion effects is readily understandable, since they correspond to actual physical vibrations in the basilar membrane.

However, the phenomenon of the *intermediate* tone is apparently not accounted for by such analyses. Its explanation must be sought in some peculiarity of the action of the basilary apparatus, when the latter is excited by two closely similar frequencies of about equal intensity. Under these conditions, we should expect to find an intermediate section of the membrane which is vibrating at both of the given frequencies at once, or within which there is incomplete tonal analysis. The beat pulsations would exist solely in this intermediate section, since in the outlying or marginal sections the frequencies would be separated from each other. The intermediate tone can perhaps be attributed to this overlapping compromise vibration, which will have an apparent frequency intermediate between those of the other two sections. When it gives rise to a separate representation in consciousness, this representation will naturally carry the subjective beats.

366. The Basilary Basis of Fusion. — It should be noted that the above discussion of the mechanism of the ear removes the difficulties which have hitherto been raised against the Helmholtzian explanation of fusion. The existence of subjective harmonics means that beats can appear between pure sinusoidal stimulus frequencies which stand in inharmonic relationships to one another.[554] Moreover, our concept of a pure tone must naturally be adulterated with that of its harmonics, as "subjectively" generated. It is not necessary to appeal, as Ogden does in a similar argument, to the familiar presence of such harmonics in musical sounds. The octave provides the most perfect consonance, because it corresponds with the subjective harmonic which is represented most loudly. The phenomenon of *octave quality,* or the marked resemblance of tones which stand in an octave relationship, can evidently be accounted for on the same basis: of common constituents; at the same time, the difference tone which it produces, in combination with the fundamental, is identical with the latter. Similar principles apply, to a lesser degree, to the third, fifth, and higher harmonics, which become less consonent in the order given.

367. Basilary Foundations of Vocables and Noises. — The consideration of the basilary response to vibrations which yield subjective beats, introduces us to the problem of what happens in the case of very complex combinations of frequencies, such as the stimuli to noises and vocables. Under the action of such forces, there will presumably be long sections of the membrane which are excited simultaneously by a number of overlapping frequencies, so that there is no clear-cut spatial separation of the component vibrations. This condition is associated with the absence of analysis in experience, and with the qualitatively unique character of the experiences themselves. In general, we may correlate the non-tonal quality of the auditory experience with the exact pattern of distribution of the amplitudes over the basilar membrane, although the departure of the hair-cell impulses from even temporal spacing is also probably involved.

For each characteristic pattern, there is a corresponding over-all quality in consciousness. These qualities may have certain resemblances to pure tonality — as in the case of the vowels — which are to be attributed to distributions of amplitudes in the membrane approximating those for some pure pitch. In general, it may be noted that pure sinusoidal vibrations are unnatural forms of stimulation, the products of musical or scientific invention, so that the normal psychophysiological relationships are probably those between qualitatively unanalyzable auditory presentations and a corresponding membranal "*Gestalt*."

Section 65

AFFERENT NEUROLOGICAL RELATIONSHIPS OF AUDITORY EXPERIENCE

368. Audio-Frequencies in the Nerve Impulse. — The next step in our discussion leads to a consideration of the psychophysiological relationships of the impulses or currents which are generated in the fibres of the auditory nerves. In discussing these relationships, we must recognize the "all-or-none" principle of nerve action, according to which each nerve pulse is normally invariable in intensity; and, secondly, the limits of frequency which are imposed upon a series of such pulses by the refractory phase characteristics of the nerve fibre excitations. In attempting to infer the relationships between features of the nerve excitation and the psychical factors, we must deal with the known general properties of nerve action, in combination with the ideas which have been established above regarding the mechanism of the sense-organ, and the relation of its processes to consciousness.

Helmholtz regarded a "place theory,"[555] of the type of his individual resonator hypothesis, as essential to an understanding of Ohm's law, and for consistency with the Müllerian doctrine of specific nerve energies. However, the fact that auditory localization can be based upon phase differences between the two ears, shows that something which is very closely similar to the actual audio-frequency must be transmitted along the nerve fibres. This seems to be true at the limit of audibility, even for the highest frequencies.

Neurologists now place the limit for the highest rate of restimulation of a nerve at about 2000 pulses per second, but we have no specific data on the human auditory fibres, and it is notorious that these temporal characteristics vary widely from one nerve species to another. (*Cf.* page 39, above.) Consequently there seems to be no sufficient reason why we should not accept the apparent implications of the localization principles, and say that, up to some very high frequency, the number of individual nerve impulses in any auditory fibre is equal to the number of vibrations executed by the corresponding section of the basilar membrane per unit of time. The two processes are synchronized, except for the usual propagational lag.

If it should turn out that single auditory nerve fibres are physiologically incapable of carrying the higher range of frequencies which yield pitch variation, we may still suppose that such frequencies can be conveyed by a *group of fibres* acting together. Thus, if the limit for a single conductor is 2000 per second, a group of five conductors can carry a frequency of 10,000, if fibre number one of the group picks up the first impact, number two the second impact, and so on. I have discussed the details of this hypothesis, together with other aspects of auditory theory, in a paper,[556] to which the reader is referred for a more elaborate treatment of the problems of auditory sensation.

Now, this assumption that the audio-frequencies are taken up by the nerve fibres does not necessarily mean that the ear is relieved of the duty of *frequency analysis*. If the actual frequencies are transmitted to the brain, it is, of course, conceivable that the analysis should occur in the latter place, although we are not acquainted with any neurological mechanism by which it could be accomplished. However, the foregoing discussion has shown that analysis probably *does* take place in the ear, so that the brain is relieved of the task, even though it may be provided with the requisite data. We should note that tonal analysis is a rather uncommon phenomenon, which applies only to relatively artificial stimuli. We may reasonably doubt whether it has any important function, *as* analysis, and may regard it as a corollary of some more general biological requirement. When the stimuli are of the musical type, the several component frequencies are transmitted along distinct groups of nerve fibres, and hence are readily separated in the cerebral cortex

369. Neural Foundations of Auditory Quality. — However, when the stimulus is more complex in composition, several different frequencies may act simultaneously upon the same nerve fibre, and in this case there will be a failure of analysis. There will also be a departure from true tonal quality. The result in consciousness will be a characteristic vocable or noise.

We are thus led to the hypothesis that the essential correlate of tone, in an auditory nerve path, is the presence of a series of evenly spaced impulses, and that the pitch is determined by the temporal frequency of these impulses. Departure from even timing means departure from tonal quality. The identity of the nerve paths is essentially immaterial. At low amplitudes of vibration of the basilar membrane, each frequency will be quite narrowly restricted to a specific group of nerve fibres — perhaps to a single fibre, at the absolute threshold — but, with augmented local vibration of the membrane, an increasingly wide band of fibres will be excited, in synchronism, at the same frequency. If the identity of the fibres were involved in the determination of pitch, we should expect this increase in the width of the band to involve a mixture of adjacent pitches, which is not the case. Moreover, according to Fletcher,[557] local degenerations of the basilar membrane never produce total deafness to the frequency which finds its normal maximum in this region. If the intensity is raised sufficiently to excite fibres outside of the affected region, the tone which appears in consciousness is characteristic of the given frequency, and not of the location of the excited fibres. The failure of pitch to change with intensity has similar implications.

370. The Neural Correlate of Loudness. — Let us next consider the case for *loudness*. Helmholtz supposed that loudness could depend upon the intensity of stimulation of a single nerve-fibre, but the all-or-none principle forbids this assumption. Of course, impulse frequency might be substituted for nerve current strength in Helmholtz's theory, but we have already employed frequency as a determinant of pitch. Apparently, therefore, we are forced to the alternative suggested in Max Meyer's hypothesis, that loudness is correlated with the total number of fibres which are stimulated, at the given frequency. We have already seen that this number increases with the degree of response of the membrane. After the amplitude of displacement of the membrane, at any point, has exceeded what is required to excite all of the local fibres, a further increase in this amplitude is without influence upon the excitations of these fibres, considered by themselves. Of course, it is likely that the various fibres will have somewhat different thresholds, so that, as the amplitude increases, there may be an increase in the total number of excited fibres, not due merely to the lateral spreading of the action, but to the picking up of those which have a higher threshold. But this does not affect the general principles which are involved.

Now, neurology suggests that if loudness stands for the total strength of nerve influence, of any given kind, it may be correlated with the total number of impulses in unit time, rather than with the number of coexcited fibres, alone.[558] If there is an accumulative or averaging effect in the brain centers, this should treat frequency and number of contributing paths somewhat similarly. For this reason, and another which will appear later, we shall adopt the view that loudness is a function of the *total number of pulses per second,* regardless of whether they are due to a multiplicity of paths or to frequency. This evidently means that more paths will be required at low than at high frequency, to yield the same loudness. The loudness of any component tone in a clang is to be attributed to the total nerve current, at the corresponding frequency, in isolation from those at other frequencies, which will normally be carried in separate bundles of fibres.

371. Neural Conditions for Noise. — The next step is to consider in greater detail what probably happens when there is inadequate separation of this sort between two adjacent frequencies. The simplest case is, perhaps, that of two sounds having frequencies such that they yield audible beats. If they are very close together, practically all of the nerve fibres in the stimulated band will be excited at both frequencies, but the deviation of the nerve-pulse rate and spacing from that for either of the frequencies, separately, may be insufficient to introduce any detectable change in the auditory experience, except for the rhythmic variation in loudness. When the stimulus frequencies are farther apart, there will be two bands of fibres which are excited exclusively at the frequencies in question, and an intermediate band which is subject to a complex action. There will be a tendency for the pulses in this *overlap band* to depart from uniform spacing, but whether or not this actually happens must depend upon the exact character of the complex wave-form which is acting upon them. A periodic vibration with large maxima, combined with small ripples or kinks, might arouse a current in the nerve fibres representative only of the larger excursions, and these might still be quite uniformly spaced.

However, we may suppose that when deviations from uniformity actually occur in the nervous pulses, the corresponding consciousness has a non-tonal character, yielding noise or some feature of a vocable. The roughness which accompanies high frequency beats can be attributed to this principle. Owing to the overlap of the bands of "subjective" harmonics, even pure sinusoidal stimuli yield noise at extremely high intensities. In the case of actual noise stimuli, the highly complex, and sometimes continuous, spectrum introduces a predominance of this kind of action, so that there may be no nerve fibres at all which are carrying evenly spaced series of impulses, and the effect of tonality may be almost completely absent. However, it will ordinarily be possible to trace some similarity between the patterns of the impulses and those due to certain pure sinusoidal stimuli.

In general, we should expect the variations in quality among auditory experiences to follow a system similar to that which is characteristic of nerve-pulse patterns of the sort just indicated. However, the total qualitative character must be correlated not only with the temporal arrangement of the impulses in individual fibres, or groups of fibres, but with the spatial distribution of these various time patterns among the fibres, in the order of their attachment to successive points on the basilar membrane. Even when there is no neurological overlapping, the various frequencies which are delivered by separate channels ordinarily yield a unified psychical resultant. The readiness with which this resultant decomposes, under the analytical attitude, must be determined by the degree of isolation of the separately excited bands, along the membrane.

372. **Neural Foundations of Brightness and Volume.** — It may appear from the above discussion that the distribution of basilar amplitudes over any single excited band can have no representation in the resulting nerve currents. However, more careful thought indicates that, in the portion of the membrane which has the greatest vibration amplitude, the nerve cells will be brought up to threshold stimulation sooner, in each cycle, than will those in a position which corresponds to lower amplitudes. Consequently, there should be a sort of *curvature of the neural wave-front* within the group of fibres which correspond to the given excited band. This effect might be used as a cue for the exact exciting frequency, in an exclusive "place theory," but since this function is not required, we may regard it as providing the neurological basis for the attribute of *brightness*. Following Ogden's ideas, as already outlined, the brightness should increase with the degree of wave-front curvature, or the "saliency" of one portion of the impulse group as compared with other portions. This saliency is not in the frequency-pitch dimension, as Ogden tends to conceive it, but in the allied dimension of analytical separation or preëminence. Bright tones have a feature of internal sharpness which is lacking in dull tones.

We still have the problem of the neurological correlate of *volume* to solve. It will be recalled that volume increases with loudness or intensity (acoustic loudness), and decreases with frequency. If we adopt the view of Boring,[559] that the direct psychophysical determinant of volume lies in the spatial dispersion of the nerve excitations in the cerebral cortex, the relation of volume to intensity is explicable in terms of the increase in the number of synchronously active nerve fibres, due to the spreading of the excited band, with increasing basilary vibration. The decrease of volume with increasing frequency can be accounted for, on this basis, as follows: We have supposed that loudness is determined by the total number of impulses arriving at the cortex per second, regardless of the number or identity of the fibres along which they come. Hence, a larger number of fibres will be required to yield any specified loudness, at low frequency than at high. Consequently, if the central dispersion depends upon the number of coexcited fibres, we should expect to find a greater volume, at constant loudness, for low than for high frequencies.

Thus, from the standpoint of the auditory nerve, volume is determined by the number of fibres which are simultaneously excited, loudness by the total rate at which unit pulses pass any fixed cross-section of the nerve, pitch by the uniform spatial separation of the unit pulses along the fibre length, brightness by the timing relations of corresponding pulses in different fibres, noise and other deviations from tonality by departures of the pulse spacing from regularity, and general quality by the total temporal and spatial ensemble, or *Gestalt.*

Chapter XVI

The Chemical Senses

Section 66

OLFACTORY SENSATION

The olfactory sense is undoubtedly the oldest of the "distance receptive" mechanisms, from the phylogenetic standpoint. As we have previously noted, it is in an anatomically as well as a physiologically decadent state in human beings. However, the intricacy of its psychophysical relationships may be reminiscent of its long, and probably complex, evolutionary history. The fact remains that these relationships are of a very puzzling character, which thus far has resisted satisfactory analytical treatment. The olfactory sense presents a number of paradoxical aspects. Although olfaction provides the evolutionary foundations for the development of the cerebral hemispheres, the most complex of neurological organs, the sensory cells are of the most primitive known type. They are practically identical in structure with the receptors which are found in the epithelium of the earthworm. It would thus seem likely that their mode of response should be quite simple, an expectation which is further supported by the fact that they are apparently all alike, anatomically. Their connections to the brain are singularly direct, since they give off integral fibres, which pass immediately into the olfactory lobes of the cerebral cortex, without peripheral synapses of any sort. Yet, the resulting experiences show an almost infinite variety. The introspective analysis of olfactory experience has been presented in Volume I. (See also, Note C, below.)

373. The Action of Odorous Vapors in the Nose. — As we have already noted, our present knowledge does not furnish us with any reliable information regarding the nature of the olfactory stimulus, if the latter is interpreted as being the exact manner of action of the vapors upon the receptors. Of course, we cannot have the slightest doubt that particles of the specifically odoriferous chemical substances must actually pass into the upper cavities of the nose, and come into contact with the olfactory sense-cells. Under ordinary conditions, these particles are in a gaseous, or vaporous, form, which means that they consist of individual molecules, dispersed among the molecules of the air. Experiments have been made by Weber,[560] Aronsohn,[561] Haycraft,[562] Varess,[563] and others to determine whether the olfactory epithelium can be stimulated by odorous substances carried in solution. It might be thought that the epithelium would normally be coated with moisture, and the relation of the olfactory sense to the chemical sense of fishes suggests that an aqueous medium might be even more favorable than an aerial one. However, it seems to be quite definitely proven that the human olfactory cells do not respond at all adequately under such conditions.[564] This may be attributed, perhaps, to a desensitization of the receptors, due to contact with the water or, on the other hand, it may indicate that a true gaseous state of the stimulus is essential.

Haycraft[565] is of the opinion, furthermore, that the odoriferous substances must not only be in a gaseous condition, but must also be in motion over the olfactory epithelium. However, it is highly probable that his experiments merely show that a considerable amount of agitation, similar to that which is produced by sniffing, is required to carry the vapors into the special chambers of the nasal cavity that contain the olfactory receptors. (See Fig. 82.) The physiological experiments of Paulsen,[566] Zwaardemaker,[567] Francke,[568] and others indicate that the normal processes of inhalation and exhalation disturb the air in these chambers relatively little. Probably no more motion is required than that which will bring the molecules into actual contact with a considerable number of receptors or the hairlets which they bear. The amount of agitation which is demanded for threshold stimulation will naturally depend upon the concentration of the odoriferous molecules in the inhaled or exhaled air; and at relatively high concentrations no special agitation will be needed. Diffusion may be sufficient, without the aid of the convection.

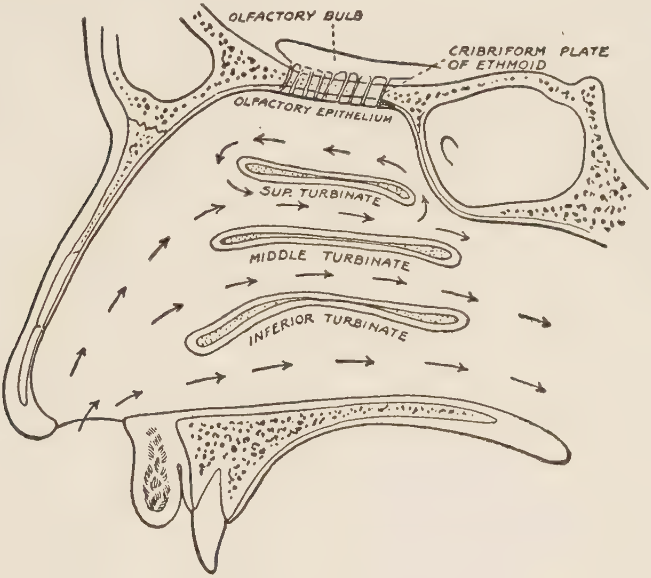

OLFACTORY BULB
CRIBRIFORM PLATE OF ETHMOID
OLFACTORY EPITHELIUM
SUP. TURBINATE
MIDDLE TURBINATE
INFERIOR TURBINATE

FIG. 82. SECTION OF THE HUMAN NASAL PASSAGES.

This figure shows an antero-posterior section through the human nasal fossal and indicates the manner of passage of the air currents during inspiration. The position of the olfactory epithelium and its connections with the olfactory bulb are represented. (*From Starling's Human Physiology; Churchill.*)

OLFACTORY INTENSITY AS A FUNCTION OF STIMULUS ASPECTS

Any particular olfactory quality can exist at various intensities, forming a continuous scale. Such subjective intensities are functions of at least three different aspects of the stimulus material: (1) its chemical identity, if it is a chemically pure substance, (2) its concentration in the air within the nasal cavity, and (3) its composition in terms of the relative concentrations of component pure chemical substances, if it is a mixture.

374. **Chemical Determinants.** — *Position in the Periodic Table.* — We have already seen that many substances are quite inodorous at all concentrations. It was noted by Ramsay [569] that, apparently, a substance must have a molecular weight which is at least fifteen times as great as that of hydrogen, in order to be odorous. All of the lighter gases, including hydrocarbons, are without effect upon the olfactory sense. Haycraft [570] pointed out that practically all odorous compounds contain elements belonging to three adjacent groups of the periodic table of the chemical elements, usually designated as the fifth, sixth, and seventh groups, respectively. Characteristic members of these groups are: for the fifth, phosphorous, arsenic, and antimony; for the sixth, sulphur, selenium and tellurium; and, for the seventh, flourine, bromine and iodine. There is a tendency, within each group, for alternate members to show an increased olfactory power. The only exceptions to Haycraft's rule are cases of organic compounds, involving carbon and hydrogen only, the aliphatic and carbocyclic hydrocarbons (such as gasoline and benzol, respectively).

Formation of Organic Compounds. — It is notable that these odor-forming elements lie wholly on one side of the periodic table with respect to the group which contains the element, carbon, the central constituent of living matter. If we exclude the anomalous group containing iron and its congeners, on the one hand, and the inert gas group (and hydrogen), on the other hand, we have a balanced system about carbon, with all of the odor-forming elements on one side. The elements in question are uniquely characterized by the possession of valences with respect to hydrogen which are different from those with respect to oxygen. The valences of the odor-forming elements are higher with respect to oxygen than are those of carbon, and they have lower valences with respect to hydrogen than has carbon. Since hydrogen and oxygen are essential coconstituents of organic substances, with carbon, it is likely that these relationships indicate that certain types of structural combination with organic matter are required in order to produce an olfactory stimulus.

This idea is confirmed by the experience of the organic chemist, which shows that the odor-forming elements are capable of entering into organic compounds, as integral constituents, whereas the elements occurring in periodic groups below carbon (with the exception of hydrogen, which is a group by itself) play a relatively inferior rôle in organic chemistry. On the whole, it seems highly probable that all immediately odorous substances belong in the class of organic compounds. On this assumption, inorganic substances, such as chlorine, ammonia, hydrogen sulphide, phosphorus, etc., must combine with the tissues or fluids of the olfactory membranes, to form definite organic compounds, before they can stimulate. The subjectively determined groups of odors, which we have considered in the chapters on perception, all refer to classes of organic, rather than of inorganic, substances. Thus, in Henning's scheme (see Note C), fragrant, ethereal, spicy, resinous, putrid, and burned are obviously indicative of different kinds or conditions of vegetal or animal tissues.

Physicochemical Properties. — It has been noted by Erdman[571] that many highly odorous substances, such as essential oils, are extremely soluble in liquid air. It is possible that this is indicative of some special relationship to oxygen or nitrogen which is involved in the stimulation of the olfactory end-organs. Tyndall[572] also remarked that the vapors of many such substances have a high degree of absorption for heat rays, which is a characteristic property of water and water vapor.

Odors of Organic Series. — Particular interest attaches to the study of the olfactory relationships of those classes of odorous organic substances which form graded series, from the chemical standpoint. Consider, for example, certain series of homologous aliphatic compounds, such as methyl, ethyl, propyl, butyl, and amyl ethers, alcohols, or esters. In such series there are progressive changes in the ability to arouse olfactory response. Thus, in the case of the alcohols, the threshold is high at the methyl end, decreasing rapidly, as the weight of the molecule increases, as shown in the following table:

TABLE XII[573]

Olfactory Thresholds

Methyl alcohol	1.0
Ethyl alcohol	0.25
Propyl alcohol	0.01
Butyl alcohol	0.001
Amyl alcohol	0.0001

However, at a still high molecular weight, the threshold is again increased, possibly due to loss of volatility. These facts indicate that the relationship between the constitution of the odorous substance and the receptor mechanism is very specific, depending not only upon the nature of the contained elements and general configuration of the molecule, but also upon its mass.

375. Olfactometry and Absolute Thresholds. — Zwaardemaker[574] invented an instrument and a method for what he called olfactometry, which involves a determination of the absolute thresholds for olfactory stimulation by different substances. However, his scheme is not well adapted to a determination of these thresholds in terms of the actual concentrations of the substances in the inhaled air. Fischer and Penzoldt[575] found that one part of mercaptan in fifty billion (50,000,000,000) parts of air could be detected. The weight of this substance in one inspiration under these conditions was computed to be about 0.0000000022 of a milligram. This means that, for such substances, the nose is more sensitive than is the spectroscope, as an instrument of specific chemical analysis, since the spectroscope cannot detect less than 0.0000007 of a milligram of the element, sodium, to which it shows the most sensitive response. However, the total number of molecules involved is very large in either case, as will be seen from the following computation. The weight of a single molecule of ethyl mercaptan ($C_2H_5.SH$) is almost exactly 1.0×10^{-22} grams, while that of the threshold amount is 2.2×10^{-12} grams. The number of molecules in the inspired air must therefore be: 2.2×10^{10}, or about twenty-two billion. Of course, only a very small proportion of these will actually come into contact with the olfactory epithelium. The following table shows some similar results obtained by Passy:[576]

TABLE XIII

OLFACTORY THRESHOLDS

Substance	*Threshold Concentration Milligrams per liter of air*
Essence of orange	0.001
Essence of wintergreen	0.0004
Rosemary	0.0008
Ether	0.004
Camphor	0.005
Heliotrope	0.05
Cumine	0.01
Vanilline	0.0005
Natural musk	0.00005
Artificial musk (trinitrobutyltoluol)	0.000005

376. Results of Olfactory Mixture. — When two substances are mixed and applied to the olfactory sense-organ, the result depends upon a number of distinct principles. If the substances react chemically, as is the case with ammonia and acetic acid, they may neutralize each other for purely objective reasons. On the other hand, mixtures of substances which do not combine chemically may also exhibit the phenomenon of neutralization, and this result can be obtained even when one of the substances is introduced into one nostril, and the other into the other nostril, so that the possibility of combination is strictly excluded. According to Zwaardemaker,[577] such an antagonism can be demonstrated between the following pairs of odorous bodies: (1) cedar wood and rubber, (2) benzoin and rubber, (3) paraffin and rubber, (4) wax and rubber, (5) balsam of Tolu and rubber, (6) wax and balsam of Tolu, (7) paraffin and wax, (8) musk and oil of bitter almonds, (9) volatile oils and iodoform, and (10) ammonia and acetic acid. If the concentrations are properly balanced, the intensity of the olfactory experience is zero, in spite of the presence of stimuli which would otherwise bring forth definite characteristic qualities. It is interesting that ammonia and acetic acid should be capable of neutralizing each other psychophysiologically, as well as chemically.

All of the facts which we have considered above relate to the conditions for threshold intensity or for absence of intensity, insofar as they are quantitatively expressed. Determinations of the laws governing supraliminal intensities have yet to be made. It would seem that a very fertile field for investigation is here presented, and one which should yield data relevant to a solution of the mysteries of the olfactory sense.

OLFACTORY QUALITY AS A FUNCTION OF CHEMICAL COMPOSITION

377. Olfactory Quality and Molecular Form. — Olfactory quality may conceivably vary as a function of the same factors which control intensity, *viz.,* chemical identity, concentration, and mixture proportions. Our definite knowledge in this field is limited mainly to the correlations with the first factor, although some observations have been made with respect to the third. We know that, in general, the olfactory quality tends to change with the chemical constitution of pure odorous substances, and hence we must suppose that such quality can be represented as a function of the molecular or atomic structure. The evidence indicates that the forms which are directly involved are of the molecular, rather than of the (intra-)atomic type. However, we are still very far from being able to say just what features of molecular form are responsible for the variations of quality. Substances having constitutions which are very similar in certain respects may nevertheless yield quite dissimilar odors, and odors which closely resemble each other may result from substances which seem to be very different, chemically. The meaning of these facts is probably limited to an indication of our ignorance as to significant aspects of molecular structure, in relation to the olfactory sense.

The fact, which we have already noted, that substances of low molecular weight are inodorous, or have relatively high thresholds, suggests that quality is determined by the *size* of the molecule, as well as by its form. It is particularly interesting to consider the manner in which olfactory quality varies along a series of homologous organic substances, such as the aliphatic esters. Such a series represents a quasi-continuous scale of structural variation. The correlations for the acetates are as follows:

Ethyl acetate	Acetic-ethereal odor
Propyl acetate	Acetic-(faint) pineapple odor
Butyl acetate	Pineapple-(faint) acetic odor
Amyl acetate	Pineapple odor, non-acetic

In this case there is a graded transition from one quality to quite a different one. The change can be attributed either to the increase in the size of the molecule, within the given chemical class, or to the specific structural modifications in the alkyl radical. The acetate portion of the molecule remains unchanged, but nevertheless plays an important part in determining the quality, since the corresponding series of alcohols yields quite different results, in spite of the similarity of the alkyl radicles to those of the acetate series.

A somewhat different kind of homologous series is presented by the corresponding compounds of distinct chemical elements which fall into the same group in the periodic table. Thus, the combinations of sulphur, selenium and tellurium with organic radicles yield similar and yet different odors, which vary in quality progressively as a function of the atomic weights of the elements in question. The same sort of relationship holds for the elements chlorine, bromine, and iodine, either by themselves or in combination with other elements. Chloroform, bromoform and iodoform constitute a transitional series, similar to that of the acetates, from the olfactory standpoint. These observations indicate that odor is probably determined by features of the molecular structure which vary with almost any change in constitution, although occasionally they may be reduplicated in chemically diverse substances. Olfactory quality seems to depend upon the total form and mass of the molecule rather than upon any single abstract aspect of its constitution.

378. Zwaardemaker's and Henning's Systems. — One of the most elaborate lists of olfactory "stimuli" is that given by Zwaardemaker in connection with his classification of odors. Although a great many of these "stimuli" are objects rather than definite chemical substances, it seems worth while to present the scheme at this point in our discussion.

TABLE XIV

Zwaardemaker's Classification of Olfactory Stimuli

Class I. *Ethereal odors*, due to
- a. Essences of fruits used in perfumery (apple, pineapple, pear, etc.).
- b. Beeswax.
- c. Ethers, aldehydes, ketones.

Class II. *Aromatic odors*, due to
- a. Camphoric substances: camphor, borneol, patchouli, rosemary, eucalyptol, turpentine.
- b. Spices: clove, ginger, pepper, etc.
- c. Anise, lavender, menthol, oil of fennel, arnica, thymol, chamomile.
- d. Lemon, rose, palisander, sandal wood, cedar wood, etc.
- e. Bitter almonds, hydrocyanic acid, benzoic and salicylic aldehydes, nitrobenzol.

Class III. *Balsamic odors*, due to
- a. Flowers: jessamine, syringa, lilies-of-the-valley, orange-blossoms, acacia, etc.
- b. Liliaceous effluvia: iris, narcissus, hyacinth, violet, mignonette.
- c. Vanilla, benzoin, balsam of Peru, balsam of Tolu, cumarine, heliotrope.

Class IV. *Ambrosial odors*, due to
- a. Amber.
- b. Musk, nitrobutyltoluol, ox-bile, many animal effluvia, and those of some fungi.

Class V. *Alliaceous odors,* due to

- a. Hydrogen sulphide, acetylene, vulcanized rubber, asafoetida, gum ammonicum, ichthyol.
- b. Hydrogen arsendie, hydrogen phosphide, trimethylamine.
- c. Chlorine, bromine, iodine, quinine.

Class VI. *Empyreumatic odors,* due to

- a. Roast coffee, toasted bread, tobacco smoke, pyrocatechin, guiacol, creosol, acrolein, piridine.
- b. Amyl alcohol and its homologues, benzol, toluol, xylol, phenol, creolin, naphthalin, naphthol.

Class VII. *Caprillic odors,* due to

- a. Caproic acid and its homologues, cheese, sweat, putrefying bones, rancid fat.
- b. Cat's urine, vaginal secretion, spermatic fluid, chestnut flour.

Class VIII. *Repugnant odors,* due to

- a. Solanaceae, henbane, etc.
- b. Certain bugs, ozoena.

Class IX. *Nauseating odors,* due to

- a. Carrion, cadavres, etc.
- b. Feces, scatole.

The subdivisions of the several classes indicate subjective similarities and differences, within the class.

Henning has made a definite selection of certain specific types of organic substances as characteristic stimuli for the six simplex odors of his system. (*Cf.* Volume I or Note C.) The fragrant qualities are said to be aroused by ortho-substitution products of the benzene ring, the spicy by para-substitution products, and the resinous by products due to "inner" substitution, or a joining of the valences across the ring by the substituent radicle. The ethereal odors correspond to aliphatic derivatives, having a forked chain structure in the molecule. The putrid depend upon aliphatic compounds containing sulphur, selenium, tellurium, nitrogen, phosphorous, arsenic, antimony, bismuth, etc. The burned are correlated with heterocyclic rings, containing nitrogen atoms as essential links in the ring structure. The duplex and multiplex odors are supposed to be determined by substances exhibiting two or more of these structural aspects in the same molecule, or possibly by mixtures. Macdonald[578] and Dimmick[579] find that this scheme shows only a 30–40% correlation with the facts which they have examined. However, to this degree it represents an approximation to a definite psychochemical system, which may eventually be perfected to cover all of the data. Reference may be had to the section on olfactory perception (Volume I) for typical concrete stimuli in the Henning system.

No reports appear to be available concerning the influence of concentration upon olfactory quality, except in the case of mixtures.

379. Qualities of Mixtures. — When two characteristic olfactory stimuli are mixed, they may either neutralize each other, partially or wholly, or they may yield a new olfactory quality. This latter quality will tend to resemble the qualities which are correlated with the individual constituents, by themselves, but will not be introspectively analyzable into the latter. The case is thus similar to that of "color-mixture" rather than to that of the combination of musical tones. Naturally, the mixture quality will most closely resemble the quality that is characteristic of the substance which has the predominant stimulating effect, just as in the case of color-mixture. When the component qualities are very dissimilar, the mixture quality tends to be unstable (*vide infra*) but complex mixtures — such as the majority of artificial perfumes — are more stable than simpler ones. When one constituent of the mixture is greatly in excess, its characteristic quality may completely dominate that of the other constituents, yielding a "masking effect," somewhat similar to that in audition, although without the feature of subjective analysis.

380. Temporal Relationships of Olfactory Intensity and Quality. — *Olfactory Rivalry.* — The instability of certain olfactory mixtures, to which we have just referred, consists in an alternation between the two qualities corresponding to the components of the mixture. This alternation is particularly marked in the case of dirhinal mixtures, and in this case is evidently analogous to binocular "retinal rivalry." (See page 203, above.) Fusion, or the production of a new or intermediate quality, may be realized at some moments, while at others the components are represented, separately. In the case of antagonistic stimuli, phases of complete neutralization may appear.

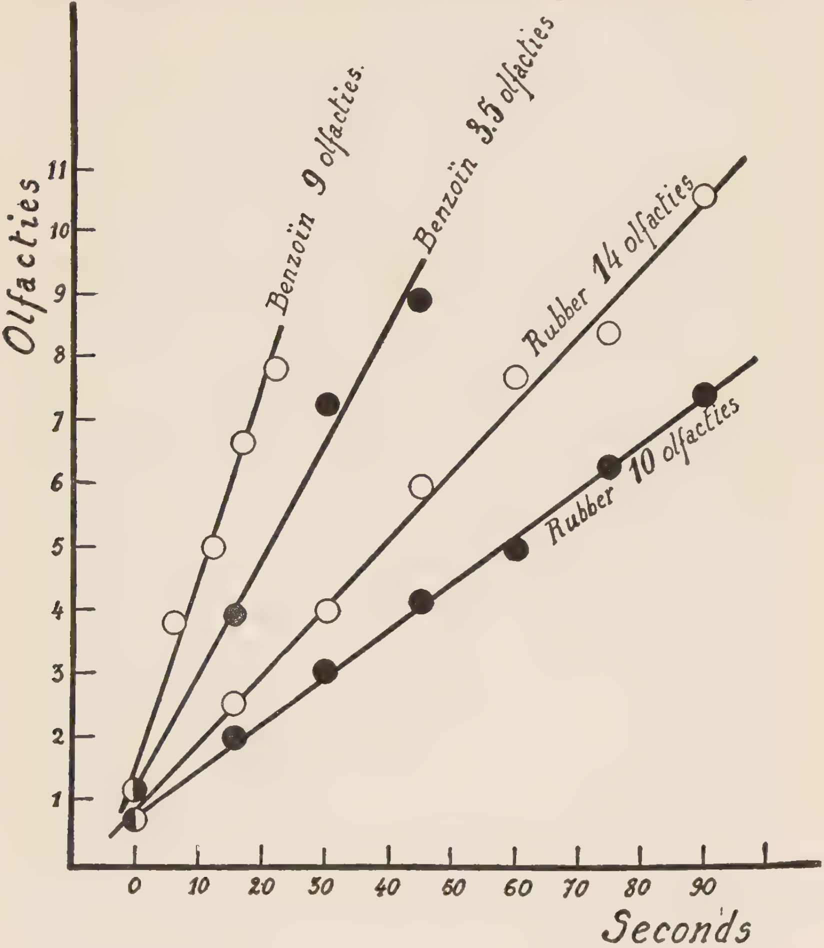


FIG. 83. CURVES OF OLFACTORY ADAPTATION.

The curves in this figure show how the absolute thresholds for olfactory response to the specified substances vary as a function of time after beginning stimulation. The thresholds and stimulus intensities are measured in olfacties (*From The Foundations of Experimental Psychology, Clark University Press.*)

Olfactory Adaptation.—Continued exposure of the olfactory epithelium to the action of a single odorous substance brings about a reduction in the sensitiveness, or an elevation of the threshold, for this particular substance. The rate at which such adaptation proceeds, increases with the intensity, or concentration of the stimulus; three to seven minutes exposure to such substances as tincture of iodine, camphor, ammonium sulphate, and turpentine suffices to eliminate the corresponding olfactory experiences altogether. As measured by the olfactometer, at relatively low intensities, the increase in the threshold follows an approximately linear law with respect to time. (See Fig. 83.) Adaptation proceeds more rapidly for certain substances than for others, even at concentrations which are the same multiples of the threshold. Recovery of sensitivity ordinarily occurs within a few minutes, but protracted exposure to fixed odors seems to produce an almost permanent, but specific, anosmia.

Such adaptation effects are definitely specific, being limited to the particular substances which are employed, or to others which are related to them. Thus, Aronsohn[580] found that, after adaptation to tincture of iodine, his discrimination of ethereal substances was unaltered, that of cedar, turpentine, bergamot, and cloves was somewhat reduced, while that of alcohol and copaiba balsam was seriously reduced. Adaptation to ammonium sulphide completely destroyed the response to hydrogen sulphide, hydrochloric acid, and bromine, but left that for ethereal substances unaffected. Zwaardemaker[581] found that the balance of a mixture could be upset by such differential adaptation. Thus, if cumarine and vanilline were combined in such proportions that the odor of the latter was dominant, adaptation to vanilline caused the mixture to smell of cumarine only. Disturbances of sensibility which are specific in this way have also been observed as permanent characteristics of certain individuals.

THE PSYCHOPHYSIOLOGY OF THE OLFACTORY RECEPTOR PROCESS

381. Review of Possible Means of Receptor Stimulation. — We have next to consider the relationships between olfactory quality and intensity, on the one hand, and the probable processes in the sensory cells and their attached conducting fibres, on the other. As shown in Fig. 84, these cells are of elongate form, bearing a number of hairlets on the exposed end, and giving rise, at the opposite end, to a fibre which makes connections directly with the neurones of the cerebral olfactory bulb. The hairlets presumably reach out into the path of the diffusing vapors, and it is natural to suppose that they receive the immediate action of the latter. There are several different ways in which we may conceive this influence to be exerted. (1) The molecules may act dynamically upon the hairs, or their enveloping membranes, without affecting them chemically. (2) The molecules may actually combine with the surfaces of the hairs, and possibly also with the exposed tips of the cells. (3) The molecules may diffuse into the body of the cell.

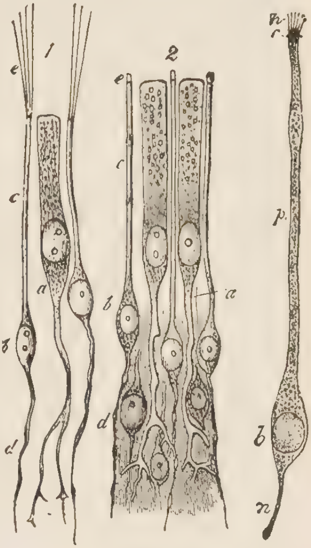


FIG. 84.
OLFACTORY RECEPTORS.
These sketches show olfactory receptor and supporting cells. The cells represented at 1 are from the frog and those at 2 from man. The drawing at the right shows an isolated human olfactory receptor cell. (*From Luciani: Human Physiology, Macmillan.*)

It has been suggested, under the first hypothesis, that each specific chemical substance, or molecule, has a characteristic natural vibration rate of its own, and that this may be imparted to the olfactory receptors. Such action might be due either to direct impact with the receptors, or to radiation emitted from the particle in the vicinity of the latter.[582] There are several serious difficulties with this type of hypothesis. In the first place, it is doubtful whether the vibration rates of molecules at physiological temperatures have a sufficient variety to account for the manifold forms of olfactory response. But an even greater difficulty appears in the extremely high frequency of these vibrations. They are all of the same general order of magnitude as those which characterize "light," and we have seen, in the case of vision, that such frequencies cannot stimulate nervous tissue directly, or be reduplicated in the processes of such tissue. It would therefore be necessary for the olfactory cells to be equipped with "photochemical" substances which are specifically responsive to certain infrared rays, in order to render this hypothesis valid.

Since the olfactory receptors are so placed as to be directly exposed to contact with the vaporized substances, there is no need for such complex assumptions. The receptors for smell provide us with the only case where an unbroken protoplasmic channel connects a material stimulus with the cerebrum. The path is so short that we are almost tempted to suppose that the actual chemical substances which are involved enter the nerve fibres and pass bodily to the region of determination of olfactory experience. If we then supposed that the olfactory quality was directly determined by the structure of such molecules, and the intensity by their concentration, we could dispense with the necessity of special representative means in the nerve impulse. Although such an hypothesis is rather too spectacular to warrant serious support, it accounts for the indefinite variety of olfactory experience, and the highly individual character of the dependencies upon specific chemical constitution. The actually valid hypothesis must have some of the properties of this scheme.

382. The Adsorption Hypothesis of Olfactory Stimulation. — The remaining alternative is to assume that the molecules actually combine with the surfaces of the hairlets, or the tips of the cells, or both; but that they do not diffuse appreciably into the bodies of the cells. Such a process of union between particular kinds of gaseous molecules and surfaces is well-known to physicists under the name of *adsorption.* It is highly characteristic of the relationship between atmospheric gases and metal surfaces, such as those of electric lamp filaments. Langmuir[583] has shown that the adsorbed substances form layers, having molecular thickness, and that the attached particles fit into the atomic mosaic of the surface in a definite pattern. The ability of the surface to take up particular molecules in this way depends upon the exact chemical relationships of the two substances which are concerned. In general, the forces which are involved in adsorption are the same as those of chemical affinity or of crystal structure. The properties of the surface are, of course, radically modified by the presence of the adsorption layer.

Now, we may suppose that in the absence of such adsorbed foreign substances the olfactory receptors are in a resting condition, but that when certain substances combine with their membranes, the latter are subjected to a depolarizing action, with consequent excitation, in accordance with the usual principles of nerve response. In order that a substance should be odorous, its molecules must have a form which is so related to that of the membrane mosaic as to permit the two systems to combine. It appears from the stimulus-experience data that a molecular weight greater than fifteen and the presence of elements in the fifth, sixth, or seventh groups of the periodic table are essential requirements. But even within the domain of these conditions there must be many variations in combining power, and in the concentrations, upon the membrane, which are required to pass the excitation threshold. A moderately high molecular weight appears to favor one or the other of these properties.

The next step is to consider how the kind and (relative) concentration of the adsorbed substance can be given representation in the nerve impulse. The first step in such an explanation is very readily taken. We must suppose that the initial depolarizing action of the stimulus produces a single nerve impulse, which is followed by recovery of excitability, and then by a second impulse, and so on. The timing of these pulses may well be determined by the nature of the adsorbed substance; in effect, each different substance will help to constitute a new and specific membrane structure, which will have chronaxial characteristics (see page 38) of its own. It is probably illegitimate to assume that such changes will affect the entire neurone, but it is sufficient that they should determine the rhythm of the responses. Intensity can, of course, be represented by the number of fibres which are simultaneously excited in the same or non-interfering ways. It is in harmony with general biological theory to suppose that the cells will react, by changes in their metabolism, so as eventually to destroy or to eliminate the adsorbed materials, and thus to restore their original conditions. This process accounts for adaptation to specific kinds of chemical stimuli, since it is in accordance with the theory of antibodies and similar chemical defense processes that the neutralization or immunity should be specific and in excess.

383. The Neural Basis of Olfactory Quality. — Antagonism between unirhinal stimuli may be referred to their concomitant action upon the membrane in such a way as to produce a null effect. It is clear that a practically infinite variety of possibilities of this sort may exist, depending upon the exact lattice pattern of the membrane, itself, and the manner in which the various molecular configurations may fit together upon it. Other stimulating substances may unite simultaneously with the membrane so as to excite it in a manner intermediate between that which characterizes the components, thus accounting for "mixture." Dirhinal antagonism and mixture must obviously be explained in terms of the combination or interference of nerve currents.

It should be clear that, in accordance with the above theory, olfactory quality is determined by the timing of the nerve pulses, while intensity will rest either upon the total number of similarly excited fibres or upon the total number of pulses per second. The timing is dependent upon the actual chemical character of the adsorbed substance, and hence may show new characteristics when new substances are applied. If we suppose this timing to be limited to the frequency of a series of impulses which are always evenly spaced, we should obviously expect to find a linear series of olfactory qualities. Such a series would not necessarily appear to be qualitatively homogeneous — like the gray series in vision —, but might show smooth variations in kind — like that which characterizes the spectral series of hues. This would yield a sort of olfactory quality spectrum with respect to nerve impulse frequency. The explanation for these changes in the mode of variation with respect to frequency would have to be sought in the total processes which are set up in the olfactory centers in correspondence with particular frequencies. (See Volume III.)

It would seem that the existence of such a linear system is inconsistent with schemes, like that of Henning, which incorporate more than one dimension of variation. However, these schemes involve the relationship of the stimulus to the nerve process as well as that of the nerve process to consciousness. It is quite conceivable that position in a linear order should be a function of any desired number of independent variables. Zwaardemaker's classification suggests a linear order more than it does any other arrangement, and Henning's scheme is characterized primarily by its lacunae. Some of Dimmick's subjects [584] preferred to arrange odors in linear order, and Juhász [585] has recently propounded the concept of "odor pitch," involving a linear arrangement of olfactory qualities, which he hopes to correlate definitely with chemical constitution.

However, the evolutionary history of the olfactory sense is so complex that we should not hesitate to assume a more intricate mechanism, if the facts actually demand it. It is quite conceivable that, although the olfactory cells all look alike, their membranes are specifically differentiated in a number of independent ways, so that some of them pick up certain classes of molecules only, while others are adsorptive of other classes. It is even possible that the separate hairlets of a single cell are differentiated in this manner, each hairlet arousing its own characteristic series of impulses, so that a complex, irregular distribution of pulses would result for the entire fibre. A similar complication of temporal relationships might follow from the simultaneous operation of differently syntonized fibres, the quality being determined not only by the frequency but by the spacing of the pulses in irregular order. Adaptation experiments, such as those of Aronsohn, seem to require component neural processes of this sort; but in their present reported form they are equally consistent with the idea that a certain section of a linear olfactory spectrum has been obliterated or depressed, which might be a consequence of a semi-specific chemical immunization of all of the cells.

Section 67

GUSTATORY SENSATION

We have seen in our discussion of gustatory perception that the primary experiential taste qualities are limited to four kinds: sweet, salt, sour, and bitter. (See Volume I or Note D.) Each of these can exist at a number of different intensities, and intermediate qualities are possible, particularly at relatively low intensities. We must now consider how these qualities, their intensities, and their intermediates are related to stimulus, receptor, and nerve path conditions.

384. The Action of the Gustatory Stimulus. — Psychophysiological experiments show that the normal gustatory stimulus consists of aqueous solutions of certain substances. Although solids and gases may bring about gustatory response, they can do so only after being dissolved in the saliva. In the state of solution, these substances are molecularly dispersed and, frequently, are ionized. Since only crystalloidal substances are sapid, it is assumed that colloidal dispersion is not adequate to put a substance into a condition in which it can stimulate the gustatory receptors. The substances, in the dissolved condition, must be brought into direct contact with the taste end-organs, and such contact is hastened by processes which increase their convection or diffusion within the mouth cavity. These include mastication, rubbing the tongue against the roof of the mouth, and the like.

385. Gustatory Quality as a Function of Stimulus Characteristics. — The quality of any gustatory experience is a function of (1) the chemical nature of the dissolved substance, (2) its concentration, and (3) the proportions of its components, if it is a mixture. Its determination also involves certain spatial and temporal factors which we shall consider later. On account of the qualitative distinctiveness of the primary gustatory qualities, we may feel justified in treating them more or less individually, rather than as mere members in a qualitative continuum.

Sweetness. — Sweet taste is evoked primarily by sugars, or organic compounds which contain the group, CH_2OH. Sugars are polyhydric alcohols, and all alcohols show a tendency to elicit sweet. However, the substance, saccharin (benzoic sulphinide), which is chemically unrelated to the sugars, is five hundred times sweeter than cane sugar, while the sugar, d-mannose, has a bitter taste. Other non-sugary substances which yield sweet include glucosides, chloroform, lead acetate, and the salts of the element, beryllium. Elements in the third, fourth, and fifth groups of the periodic table are apt to form sweet-tasting compounds. According to Puitti,[586] dextro-rotatory asparagine is sweet, while the laevo-rotatory form is tasteless. These facts indicate that the arousal of the sweet-taste receptors depends upon some arrangement of atomic or ionic units within a molecule which is characterististic of the majority of sugars, but may accidentally be reduplicated in other chemical groupings.

Saltiness. — The characteristic stimuli to salt appear to be the chlorides of the alkali metals: lithium, sodium, potassium, rubidium, and caesium. However, all of the chlorides of the elements included in Group I of the periodic table are salty. Atomic or molecular weight appears to play no important rôle in determining saltiness. The prototype of salty substances is undoubtedly sodium chloride, or common salt. The majority of so-called "chemical salts" — produced by the reaction of an acid with a base — with the exception of those indicated above, arouse a bitter or a sweet taste along with the salty. Höber and Kiesow[587] found that the salty taste of the compounds, $NaCl$, KCl, $MgCl_2$, $(CH_3)NH_3Cl$, $(C_2H_5)NH_3Cl$, $NaBr$, NaI, K_2SO_4, Na_2SO_4 could be attributed to the action of the anions which are produced by electrolytic dissociation in aqueous solution. This would indicate that the ions, Cl^-, Br^-, I^-, and SO_4^-, possibly among others, are characteristic stimuli to saltiness. The metallic ions may arouse qualities which are different from and even antagonistic to those of the anions, while the undissociated molecules are probably tasteless. It is possible that saltiness may be characteristic of negative ions, in general, when not opposed by other features of the dissociated substance.

Sourness. — Since sour is almost invariably evoked by acids, and since the latter are identified chemically by their production of positive hydrogen ions in solution, it is natural to attribute the gustatory quality in question to these ions. It is claimed by Haycraft[588] that organic compounds containing the $COOH$ group have an acid taste; but the substances which he cites also yield hydrogen ions in solution. Neutral salts and non-acids, in general, appear never to arouse the sour-taste experience.

Bitterness. — Although we regard the characteristic stimulus to bitter as consisting in an alkaloid, this gustatory quality is also evoked by many other types of substances, as already noted. Thus the sulphates of the metals in the first group of the periodic table have a bitter-sweet taste, while the chlorides of the second group metals are bitter-salty. The chlorides of the seventh group elements also yield bitter. The alkaloids are nitrogen-containing organic substances, having a basic character, and found in nature almost exclusively in dicotyledenous plants. They are usually tertiary amines, or complex substitution products of ammonia involving a heterocyclic ring structure. Acting as bases, they form salts, such as quinine sulphate, in the case of the alkaloid, quinine. In view of the evocation of bitter by certain inorganic basic ions, it seems likely that this quality is correlated with chemical structures which are of a basic, as opposed as an acidic, character.

Quality and Concentration.—Höber and Kiesow[589] found that changes in the concentration of a single chemical salt solution were accompanied by alterations in the quality of the taste. They attributed this to corresponding changes in the degree of ionization of the dissolved substance.

The Taste of Mixtures.—In general, mixtures have tastes which are intermediate in quality between the experiences which are evoked by the components. However, mixture nearly always results in a reduction of gustatory intensity, as if there were a mutual interference between the stimulus components. This interference is apparently greatest between sweet and bitter, sour and salt, and sour and bitter. It is less between salt and bitter and least between sweet and sour. When the concentrations are high, there is apt to be an alternation of the qualities which are characteristic of the component stimuli; or the primary qualities may be aroused simultaneously at separate points in the mouth cavity. According to Kiesow,[590] a certain proportion of sugar and salt at low concentrations yields an "insipid alkaline taste" resembling neither. However, it has been shown that the usual alkaline and "metallic" tastes are actually dependent upon olfactory contributions for their characteristic qualities.

386. Gustatory Intensity as a Function of Stimulus Characteristics. — The quantitative study of the manner of determination of the intensity feature of gustatory experience has been limited primarily to the measurement of absolute thresholds. It should be possible, however, to determine the laws for supraliminal intensity scales, based upon the just noticeable difference in intensity, for a wide range of chemical stimuli. Although such studies appear to be lacking, there is a considerable amount of data concerning the minimal concentrations of various substances required just to arouse their characteristic gustatory qualities. Some substances appear to have no taste, regardless of their concentrations, although they may give rise to tactual, thermal, or pain experiences within the mouth. Other substances are effective at very low concentrations, but in no case is the gustatory sense so sensitive as that of smell. Characteristic stimuli for the four primary taste qualities yield the following concentrations at threshold intensity:

TABLE XV

Gustatory Thresholds

Substance	*Threshold Concentration in grams per 100 cu. cm. of water*
Sugar (Saccharose)	0.50
Salt (Sodium Chloride)	0.25
Acid (Hydrochloric)	0.007
Quinine sulphate	0.00005

It will be noted that the order of sensibility corresponds to that required to detect the respective substances in biologically significant amounts. Alkaloids are dangerous in very low concentrations, but relatively large quantities of sugar are needed to meet the demands of muscular activity.

If we consider each of the four qualities separately, we find that the concentrations required for threshold intensity vary with the chemical substance which is employed as a stimulus. We have already noted that, in the case of sweetness, saccharine needs only one five-hundredth the concentration of saccharose to yield the same gustatory intensity. The sodium salt of saccharine, however, needs to be in one four-hundredth the concentration to give the same result. Although the change is in the right direction, this difference cannot be completely accounted for by the fact that the sodium salt has a higher molecular weight than has saccharine, itself. However, Gley and Richet[591] found that the threshold concentrations of the halides of the alkali metals (chlorides, bromides, and iodides of lithium, sodium, potassium, rubidium) are equimolecular, or involve the same number of molecules per unit volume, regardless of the molecular weight of the given substance. This suggests that the thresholds for salt, and possibly bitter, may stand in a constant relation to the concentrations of certain ions or molecular components, such as Cl^-, Br^- and I^-, when these concentrations are expressed in number of molecules rather than grams. The studies of Höber and Kiesow, already quoted, confirm this general notion, by showing that the nature of intermediate taste qualities depends upon the proportions of the various species of ions in the solution. In the case of sour, it seems highly probable that the threshold and other intensity measures can be represented as functions of the hydrogen ion concentration, alone. This is known to be highly variable for different acids and with different concentrations of any given acid. The intensity of bitter is evidently determined, like that of sweet, by the exact structure of the molecule, as well as by the concentration of some characteristic constituent of the latter. In general, the thresholds for bitter and for sweet appear to be lower, the more complex the molecule. In the cases of sour and salt, this dependency is less evident, and may be absent entirely.

387. Gustatory Quality and Intensity as Functions of Spatial Features of the Stimulus. — *Position.* — The gustatory experiences, like those of touch, temperature, and pain, have definite localizations on the experiential body surface. Within the mouth, they may be localized at different points, as at the tip or the base of the tongue. These experiential positions are correlated in an obvious manner with the positions of the corresponding stimuli within the mouth cavity. The exploration of the mucous membranes with stimuli of small area shows that gustatory qualities can be evoked only at certain definite points, which correspond in location with the so-called taste buds. These sensitive points are most numerous along the edges and base of the tongue, but can also be found on the pillars of the fauces, the posterior surface of the epiglottis and the artyrenoid cartilage of the larynx. The ventral surface and central area of the dorsal surface of the tongue (in adults but not in children), and the inner surface of the cheeks, are insensitive gustatorially. On the tongue, the sensitive spots coincide with the locations of some of the so-called circumvallate and fungiform papillae, which carry the taste-buds.

Experiments with locally restricted stimuli show that both the quality and the intensity of the gustatory experience may change with position of the receptive area, when stimulus character and concentration are held constant. Thus, between the tip and the base of the tongue, respectively, we note the following changes: with sodium chloride, from pure salty to slightly bitter; with potassium chloride, from salty to sweet; with sodium sulphate, from salty to bitter; with alum, from sour to sweet; with bromosaccharine, from sweet to bitter. Schreiber [592] showed that the areas of the tongue which are insensitive are of different shapes and sizes for the four gustatory qualities, that for sour being the smallest and for bitter the largest. (See Fig. 85.) Hänig [593] demonstrated the lowest threshold for sweet at the tip, and the highest threshold at the base of the tongue. Bitter varies in the reverse direction. Sour and salt are evoked more readily along the edges of the tongue than at the base, but sour falls off towards the tip.

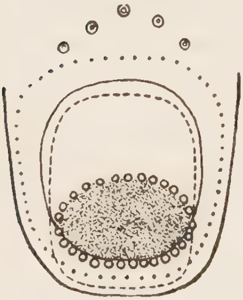


Fig. 85.
Distribution of Gustatory Sensibility Over the Tongue.

This sketch, due to Schreiber, shows the upper or dorsal surface of the tongue. The finely dotted oval area is gustatorily insensitive. The area surrounded by a line of small circles fails to evoke "sour," that surrounded by an unbroken line yields no "sweet" response; by a dashed line, no "salt"; and by a dotted line, no "bitter."

Area.— Oehrwall [594] and also Kiesow [595] have stimulated individual fungiform papillae of the tongue with chemical and electrical agencies. They found that, while many of the papillae responded with all four types of gustatory reaction, a considerable number failed to respond in one way or another, and a few responded only with single primary qualities. None were found which yielded bitter only. Papillae which failed to yield sour with an acid stimulus also failed to evoke this quality with an electrical stimulus. The manner of distribution of the four forms of taste quality among the papillae suggests that they are not correlated with one another in any fixed manner, but behave like independent, although associated, functions. However, the data of Kiesow and Hänig confirm the notion that the concentration threshold increases with decrease in the area of the receptive surface which is simultaneously stimulated, or that gustatory intensity should increase with area at constant concentration of the same substance.

Contrast. — Gustatory intensity is affected not only by the position of the stimulus but by the state of excitation of adjoining portions of the receptive surface. A concentration of sugar which is insufficient to pass the threshold, when applied to one side of the tongue, may do so if the opposite side is stimulated with acid. Similar relations hold between salt and sour, and salt and sweet, but if the subliminal stimulus is for bitter, it is said to appear as sweet, when subjected to contrast action with sweet, sour, or salt stimuli.

388. Gustatory Quality and Intensity as Functions of Temporal Features of the Stimulus. — *Reaction Times.* — The time required for gustatory qualities to appear, after the application of the stimulus, varies with the quality in question and with the position of the stimulus. At the tip of the tongue, Kiesow[596] found the following reaction times:

Sodium chloride	0.308 seconds
Sugar	0.446 "
Hydrochloric acid	0.536 "
Quinine	1.082 "

At the base of the tongue, however, there is practically no difference for salt, sweet, and bitter. In view of the greater sensitivity of the tip for sweet, and of the base for bitter, it appears that the latent period decreases as the sensitivity increases, but that, nevertheless, bitter is characteristically slower than are the other qualities. Schirmer[597] states that if a balanced mixture of four specific stimuli is applied to the tongue, the order of appearance of the gustatory qualities is: salt, sweet, sour, and bitter. There appear to be no extant data regarding the laws of "decay" of gustatory experiences.

Critical Frequency. — However, Allen and Weinberg [598] have excited the taste receptors intermittently with an electrical stimulus, and have determined the minimal frequencies for different voltages at which the gustatory experience is continuous rather than intermittent. This critical interruption frequency decreases with increasing current, and the data fall upon four smooth curves, as shown in Fig. 86. The curves conform to the general equation

$$\frac{I}{D} = -k \log Q + c$$

where D is the duration of a single impulse and Q is the current. It will be seen that the critical frequencies vary between 225 and 640 per second. The distribution of the data into four separate curves is taken to be a corroboration of the fourfold constitution of the gustatory sense.

Adaptation and Selective Changes. — The continued action of any characteristic gustatory stimulus is accompanied by a progressive reduction in the intensity of the corresponding experiential quality, although the rate and degree of this adaptation is less than in the case of olfaction. Such adaptation tends in some cases to be specific, and may lower the thresholds for other gustatory qualities. Thus, it is common experience that acid foods taste particularly sour after eating sweets. Zuntz and Heymans [599] found that exposure of the tongue to the action of a solution of sodium chloride and quinine at a concentration too low to arouse taste, definately lowered the threshold for sugar. Distilled water tastes sweet after the application of sodium or potassium chloride, or of sulphuric or hydrochloric acid. After sulphuric acid, a weak solution of quinine sulphate yields bitter at the base of the tongue, as usual, but sweet at the tip. According to Oehrwall,[600] however, exposure to bitter does not increase the sensibility to sweet, while exposure to sweet actually decreases the sensibility to acid. This latter statement seems to be opposed to common experience.

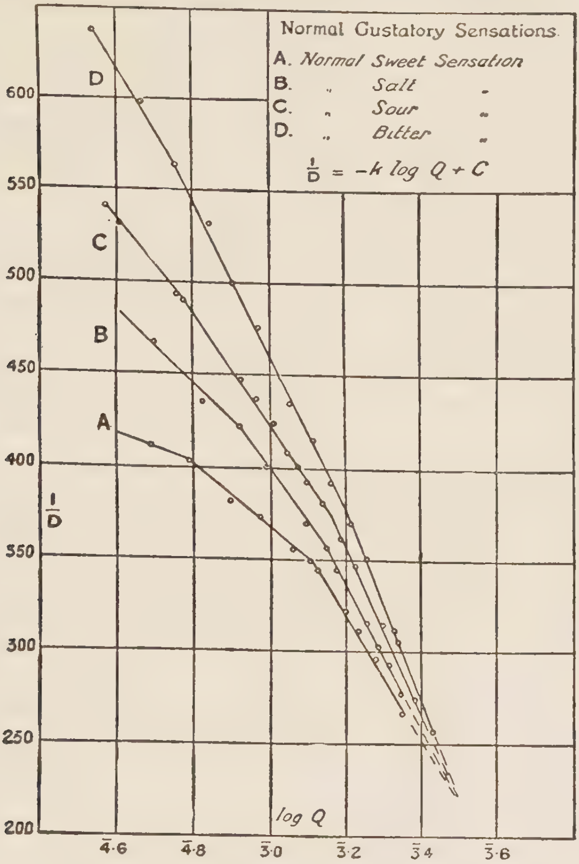


FIG. 86. GUSTATORY PERSISTENCE CURVES.

These curves, from the work of Allen and Weinberg, show how the critical fusion frequency for gustatory response to an interrupted electrical stimulus varies as a function of the stimulus intensity. The ordinates represent the number of interruptions per second, and the abscissae the logarithm of the stimulus intensity.

Some of these differential effects probably do not belong properly in the category of successive contrast. Thus the effect of sulphuric acid upon the taste of quinine is not duplicated by the action of formic, citric, and acetic acids, and hence may not be due to its acidity, alone. Certain narcotic substances produce a differential anaesthesia with respect to the four primary taste qualities. Cocaine acts most strongly on bitter, least on sweet, and to an intermediate degree upon salt and sour. Gymnemic acid, on the other hand, abolishes sensibility for sweet, and has no effect upon that for sour. Bitter and salt are affected to an intermediate degree. Stovaine attacks bitter and sweet more than it does sour and salt, while cobalt chloride causes all liquids to taste salty.

Titchener[601] holds that adaptation for any one of the three qualities, sour, sweet, or salt, increases the intensities or lowers the thresholds for the remaining two, other things equal. However, bitter is apparently left out of this relationship, in spite of its apparent antagonism with sweet in the case of mixtures. Cooling the tongue with ice-water or warming it to 40–50 degrees Centigrade practically abolishes sweet and other qualities with the exception of sour.

389. The Psychophysiology of the Gustatory Receptor Process. — *The Taste-Buds.* — The highly specialized structures of the so-called taste-buds, and their presence in the papillae — and at other points from which gustatory response can be produced — leaves little doubt that they are the specific sense-organs for taste. However, their histological details give us practically no assistance in understanding their manner of operation. (See Fig. 87.) The receptor cells consist of elongate bodies, having a single hairlet on one end, and a fibrous extension on the other end. Unlike the olfactory cells, they do not give rise to a true nerve fibre, but are enveloped in arborizations of the sensory conductors. A number of these receptor cells are grouped together in a single taste-bud, the hairlets projecting through the orifice of the latter so that they are exposed to the direct action of the sapid solutions. So far as can be determined by histological methods, the taste-buds and the individual receptor cells are all alike.

In spite of this histological similarity, psychophysiological evidence, as we have seen, strongly supports the notion that there are four different species of gustatory receptors, corresponding to the four primary taste qualities. Whether all of the receptors within a single bud are alike or different, we cannot say; but the findings of Kiesow and of Hänig[602] indicate quite definitely that all of the buds in an entire *papilla* may sometimes belong to only a single class. Since an individual taste-bud usually connects with but one sensory nerve fibre, and since the receptor cells are presumably developed from the same ontogenetic tissues, it seems likely that each bud has only a single "specific energy." The data of the investigators above referred to, indicate that the taste-bud "population" of a papilla has a random distribution with respect to the four modalities, although with a tendency for bitter never to be absent when any other modality is rep-

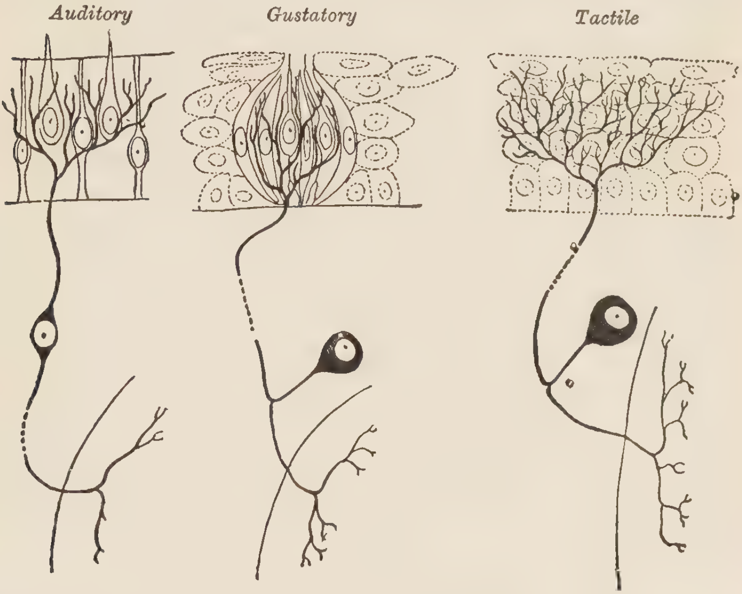


FIG. 87. TASTE-BUD AND OTHER RECEPTIVE SYSTEMS.

The middle section of this drawing shows the general structure and nerve connections of the vertebrate taste-bud. The left and right sections of the drawing show the corresponding relationships of auditory and tactile receptors, respectively. (*From Quain's Anatomy; Longmans, Green & Co.*)

resented. Titchener[603] cites a case of one papilla which was found to be sensitive only for bitter.

Specific Gustatory Membrane Structures. — We should not be surprised that there are no histological differences between functionally different gustatory cells, since the effective distinctions must necessarily be of a chemical nature. The differential characteristics must almost certainly lie in the molecular mosaic constitutions of the membranes which form the surfaces of the gustatory hairlets. These mosaics must be specific with respect to four different classes of chemical substances, standing in a "lock and key" relationship to the latter. Such a relationship, which is the basis of specific adsorptive processes — such as those of enzyme action — cannot be expected to distinguish the functionally important classes of chemical substances to the complete exclusion of all other substances, particularly if a class and not an individual is involved. Any other molecule which happens to have a similar pattern of positive and negative electrical charges upon its surface may produce excitation. Hence, there is no fundamental mystery in the fact that a body such as lead acetate can stimulate the cells which nature has designed to respond to sugars. The fact that gustatory quality may sometimes depend upon the direction of optical rotation, as in the case of asparagine, must be regarded as almost conclusive proof of the validity of this specific adsorption hypothesis. The dextro- and laevo-rotatory molecules are similar in all respects except their right- and left-handedness, but this difference is obviously all-important in a lock and key relationship.

Sour and Salt. — It seems possible to make a fairly plausible guess as to the general nature of the ionic or atomic groupings to which the four supposed types of gustatory membranes are sensitive. We may reasonably suppose that the receptors for sour and salt have a relatively simple membrane mosaic, which sensitizes them to hydrogen ions, and certain small negative ions, respectively. Hydrogen ions are already very important factors in the polarization of the enveloping membranes of living cells, so that it is not difficult to imagine a condition under which an increase in their local concentration will bring about excitation. It is of interest in this connection to note that the action of an electric current upon the tongue yields sour at the anode, at which point we should normally expect to get an increase in the hydrogen ion concentration, due to the flow of the current. However, the structure of the membrane will have to be special in order to be specifically excited by such increases. Similar lines of thought should lead us to a conception of a membrane structure which would respond in the presence of certain negative ions, such as Cl^-, Br^-, SO_4^-, in sufficient concentrations.

Sweet. — In the case of the receptors for sweet or bitter, we must deal with more complex molecular mosaics. The molecular structure of the sugars is characterized by a chain of carbon atoms, typically six, each such atom bearing a hydrogen atom on the one hand and a hydroxyl group on the other hand. At the ends of the chains, there may be additional hydrogen atoms, forming the group, $CH_2.OH$. As we have noted, sugars are classed as polyhydric alcohols, and may have either an aldehyde or a ketone formation. The fact that alcohols taste sweet is probably explicable on the basis of their structural similarity to the sugars. However, we can trace no significant structural similarity between sugars and such substances as lead acetate or benzoic sulphinide (saccharin). Nevertheless, if we were able to determine the exact distribution of positive and negative charges over the surfaces of the molecules of these latter substances, we might well find that they have certain components of pattern resembling those of the hexoses. It is characteristic of the modern view regarding chemical union, that the electrons in a subatomic structure, such as that of lead, should be conceived as being thrown into new formations as a consequence of the particular molecular combination into which they have entered, so that the ion mosaic of the atom is not necessarily distinguishable from that of the compound as a whole.

Bitter. — In the case of bitter, we might apply similar reasoning, on the supposition that the membrane mosaic is adapted primarily to the patterns of the alkaloid molecules. We know, in general, that the alkaloids have very powerful and specific effects upon nervous tissue, and this must be explained in terms of the peculiar spatial configurations of their molecules. Thus, the alkaloid, cocaine, is capable of paralyzing any sensory or motor nerve. The typical alkaloids all involve cyclic chains of atoms, at least one member of which is a nitrogen atom. They are regarded by Guareschi[604] as degradation products of plant metabolism which, being of a basic character, immediately combine with an acid or alcohol radicle. However, their action upon nervous tissue is evidently independent of such affinities; witness the instances of quinine sulphate and cocaine hydrochlorate. It must be attributed to their characteristic molecular patterns. The action of other substances, such as certain basic ions, upon the bitter receptors may be due to their simulation of certain subdivisions of these patterns, so that they can be absorbed upon the membrane at certain points, only, thus requiring a higher concentration to yield the same degree of excitation. Owing to the considerable diversity of the naturally effective alkaloid structures, there should be an appreciable amount of latitude for such action.

The basis of specific adaptation is to be sought in effects similar to those which we have considered for the olfactory receptor cells. The membranes, or the cell plasm, presumably react so as to counterbalance and to eliminate the stimulating materials, thus bringing about a temporary, relative immunity. The action of specific substances, such as cocaine, sulphuric and gymnemic acids in altering the comparative sensibilities of the various species of receptors can readily be imagined to depend upon specific reactions with the several membrane mosaics, temporarily altering their forms.

390. Neurological Correlations of Gustatory Quality. — We may feel safe in assuming that the excitation of any gustatory cell results in a pulsatory current passing along the corresponding nerve fibres, the number of quantum pulses delivered per second being responsible for the intensity factor. This number is apparently capable of summation over a considerable group of receptors and even of taste-buds. Thus, the intensity of the accompanying gustatory experience may be conceived to be determined by the number of pulses per second per unit of receptive area. If only a single species of receptors is involved, the quality will be determined by the identity of the given nerve paths, which must be supposed to have specific kinds of termini in the brain. When two or more species of receptors and nerve paths are concerned, the quality may be intermediate, in a manner determined by the proportions between the constituent neural activities. However, it appears that the central relationships of the paths in question are such as to involve a certain amount of mutual inhibition or interference. This relationship will account, also, for some of the phenomena of contrast, whether simultaneous or successive.

Chapter XVII

The Cutaneous Senses

The cutaneous senses may be divided into the tactual, the thermal, and the algesic. (For introspective analysis, see Volume I or Note E.) The first, the sense of touch, presents a number of different aspects, including contact, tickle, and the so-called "vibratory sense." Thermal sensibility embraces the two distinct modalities of warmth and cold. The algesic sense of the skin should probably be construed to include that of itch as well as of surface pain, and is to be distinguished from the numerous other pain processes of internal organs. The term "skin," in the present context, is not limited to the outer dermis, but applies also to the mucous membranes of the bucal and anal ends of the alimentary canal, the nose, the genitalia, etc.

391. Head's Theory of Protopathic and Epicritic Sensibility. — Observations upon the sensory phenomena which accompany the gradual regeneration of a severed cutaneous nerve have led Henry Head [605] to advocate the doctrine of a dual system of cutaneous sensibility, each phase of which includes all of the above modalities. He distinguishes, in the first place, between *deep sensibility,* which remains after the cutaneous nerve has been cut, and cutaneous sensibility proper. The deep sensibility is to be attributed to proprioceptive and allied channels. It mediates the qualities of pressure and of pain but not of temperature, and makes possible an accurate localization of the stimulus, without, however, permitting of discrimination between double and single contact, unless the two points are applied successively.

The cutaneous system proper is divided into the so-called *protopathic* and epicritic components. The former is the first to appear in the process of nerve-fibre regeneration. It is characterized by a sharply punctate distribution of the sensibility, but — paradoxically enough — by poor localization and a high two-point threshold. The protopathic temperature system responds to cold below 26° C. and to heat above 38° C., but not to intermediate values. As judged by the introspective phenomena, its reactions are of an all-or-none character, and the system is practically non-adaptive to sustained high or low temperatures. Pain response is also present. According to Head, the experiences which accompany protopathic excitation have a vivid, irradiating character. The tactual quality closely resembles tickle and is confined to the region of the hair roots.

During the slow progress of nerve-fibre regeneration, the protopathic condition may continue over many months, but when the supposed *epicritic* system begins to become effective, there is a rather sudden change in the sensory process. The irradiating qualities of the protopathic system are repressed, the sharply punctate distribution of sensibility is supplemented by a more continuous response, and the gap between 26° and 38° C. in the thermal scale is filled in. At the same time, ability to localize and to detect doubleness of contact is greatly improved. The temperature system becomes adaptive, and, in general, the intensity of the response becomes more nearly proportional to that of the stimuli.

Head believes that the protopathic condition represents a permanent system of cutaneous sensibility which coexists, even in the normal state, with the more advanced epicritic system. Ordinarily, for the majority of bodily areas, the epicritic system represses the protopathic one, presumably by a thalamic mechanism. However, certain skin areas, such as the glans penis, show a pure protopathic response, even under normal circumstances. Special conditions of stimulation, such as those giving rise to tickle and itch, are supposed to be capable of bringing about a functional isolation of protopathic excitation.

392. **Criticisms of Head's Theory.** — Although Head's doctrine of the protopathic and epicritic systems was gen-

erally accepted by psychologists when it first appeared, subsequent experimental and critical examinations of the theory have led to its rejection by the majority. Head's experiments have been repeated by Trotter and Davies[606] and by Boring,[607] while pertinent observations in the same field have been made by von Frey,[608] Pollock,[609] and others. Head's critics confirm most of his experimental findings, but believe that the phenomena can be adequately explained in terms of the continuously graded regeneration of a single cutaneous system. Carr[610] points out that Head's own data can be interpreted in terms of seven systems even more legitimately than in terms of two. The anatomy of the cutaneous nerve supply, with its multitude of histologically different receptors, suggests that an even greater complexity may well exist. Protopathic touch, according to Head, consists in the tactile response of the receptors at the hair roots, and this system can readily be distinguished anatomically from that which involves the Meissner corpuscles of the hairless regions.

Head's views suffer from certain psychologically paradoxical features, in which their author seems to glory, but which it is certainly desirable to eliminate, if possible. Thus, the same system is said to show accurate localization but complete inability to distinguish doubleness. Boring[611] found, in his experiment, that with sufficiently heavy pressure, the system of deep sensibility yields a perfectly definite two-point response. Localization and doubleness may well be separate functions for the cerebral cortex, but it seems unlikely that they can be separated in the peripheral nerve conduction. The notion of the protopathic system as having a non-punctate distribution also seems inconsistent with the necessarily spotted localization of the receptors. Boring also found that two-point discrimination exists in the protopathic stage and improves continuously with advancing nerve regeneration.

Boring's explanations of the characteristic phases of return of sensibility, in the nerve regeneration experiment, seem to me to account for the facts in terms of the progressive restitution of a generally homogeneous system. Consequently, in the ensuing discussion, I shall disregard Head's distinction between protopathic and epicritic components.

Section 68

THERMAL SENSATION

We have seen in our discussion of thermal perception (Volume I and Note E) that there are two distinct qualities of thermal experience, those of warmth and coolness, respectively, each being capable of variation in intensity. Under ordinary conditions, they are mutually exclusive and behave as if constituting a single algebraic variable. An apparent exception to this principle exists in the case of the so-called "paradoxical cold," although, even in this case, the conscious quality departs from that of normal coolness. We must now consider the functions which relate these two qualities, and their intensities, to stimulus, receptor, and nerve conduction factors.

393. The Definition of the Thermal Stimulus. — We have already noted that the bodily condition for thermal experience consists in a departure of the temperature of the skin from a standard value which is known as the *physiological zero*. Evidently, therefore, the stimulus to such experience or response must be defined either as *a temperate difference* or as *a rate of change in temperature.* On the first basis, we might write:

$$S = T - T_0,$$

where S is the stimulus magnitude, T is the given skin temperature, and T_0 is the physiological zero. The latter is a constant only for the given time and place, although its variability is distinctly limited in range. It may be considered as approximating the normal or usual temperature of the particular portion of the body which is concerned. Thus, for the hand it may be about 32° C.; for the lobe of the ear, about 29° C.; but for the tongue, 37.6° C. It will not ordinarily exceed this latter value, which is the normal blood temperature. Parts of the body which are habitually protected by clothes will tend to have higher characteristic values of T_0 than will portions which are exposed.

It was claimed by Weber,[612] on the other hand, that the stimulus to thermal response consists in a rate of change of temperature, rather than in a static difference. This would demand a formula of the type

$$S = d(T - T_0)/dt,$$

where dt is the differential of time. This view was based upon the fact that if a temperature difference is established very slowly, it may be ineffective, even when it would yield response at a higher rate of change. However, the phenomena in question can equally well be accounted for by supposing that T_0 is not constant but itself tends to change, with time, in accordance with a law of the form:

$$\frac{dT_0}{dt} = K\,(T - T_0)$$

which implies that T_0 will decrease if $T < T_0$, and will increase if $T > T_0$. Since the facts are in favor of a law of this general type, operating within certain restricted limits of temperature, the Weber definition of the stimulus can be disregarded. In case the temperature difference is relatively small and is slowly applied, the change in T_0 may prevent S, in our first formula, from exceeding the absolute threshold. We may assume in our definition of the stimulus, as a temperature difference rather than as a rate of change, that the increment or decrement of temperature is instantaneously effected, although in practice, a finite rate of change must be involved, and hence some change in T_0 with respect to its starting value.

In our discussion of thermal perception (see Volume I), we have already considered the various factors which control the temperature and changes in temperature of the skin. For the purposes of sensory theory, a knowledge of these principles may be assumed, or may perhaps be regarded as irrelevant.

394. Thermal Experience as a Function of Temperature. — It will be noted that the definition of the stimulus to thermal response as a difference, makes negative as well as positive values possible. Thus, if $T > T_0$, the value will be positive, or if $T < T_0$, it will be negative. With the exception of the case of paradoxical cold, it is a rule that the warmth experience accompanies positive values of S, while the coolness experience goes with negative values. In general, the intensities of the two qualities increase as the arithmetic magnitudes of S increase, for the respective cases.

The first question is as to the amount of departure from physiological zero which is required to yield a just noticeable thermal quality or intensity. This constitutes the "absolute threshold" in this particular sense department, although consisting actually of a difference and not an absolute temperature value. Culler[613] finds that when large areas of the skin of the hand are stimulated, this value can be as low as 0.03°–0.05° C. The threshold is at a minimum when the effective physiological zero, or adaptation temperature, is at about 28° C., increasing on either side of this temperature, as a linear function of the degree of departure from the latter, to values of about 0.08° C. at either 16° or 44°, where pain and numbness begin to appear. The threshold for a just perceptible cool is practically the same as that for a just perceptible warmth, so that the interval between the two threshold points is about double the absolute threshold for either modality, taken separately. The minimum value for this interval of thermal indifference was found to be 0.071° C. (at 28° C. adaptation level).

Other investigators, without paying definite attention to the state of adaptation, or the effective physiological zero, have found values ranging between 0.2° and 1.2° C. for the just noticeable difference in temperature, on various portions of the body surface. The first figure is given by Nothnagel[614] for the fingers, and the last for the middle line of the back, while the palm of the hand was found to yield a value of 0.4° C. According to Culler, the differential threshold, in the case of the whole hand, is very much higher than the absolute threshold, his own values varying rather irregularly in the vicinity of 0.3° C., when the hand is adapted to 32° C., and over a range from 20° to 48° C. The magnitude of the threshold does not follow Weber's law, although it tends to increase as the stimulus temperatures depart from the adaptation temperature or effective physiological zero. At high temperatures, the sensibility is apparently increased due to the appearance of the pain response. Culler believes that the differential threshold is a direct measure of the rate at which adaptation is proceeding, while the absolute threshold is an inverse measure of adaptive capacity at any given temperature. Earlier investigators found regions of maximal temperature sensibility between 12.5° and 25° C. (Fechner) and 35°–39° (Alsberg) and 27°–33° C. (Nothnagel), the discrepancy between these results evidently being due to neglect of adaptation conditions.

Paradoxical Cold and "Heat." — At temperatures lying between 45° and 50° C. the cold quality can be evoked by a stimulus which can also excite the warmth receptors. The exact temperature for the production of this "paradoxical cold" varies with the location on the body surface and with the state of adaptation. The effect is most definitely demonstrable with small stimuli which can be applied to individual "cold spots" so that concurrent evocation of warmth does not occur. Burnett and Dallenbach[615] have shown that the experiential quality called "hot" is referable to a combination of the response of warmth receptors with that of paradoxically aroused cold receptors. Since this combination is not realized until a temperature of 45° C., at the lowest, is reached, and pain may supervene at 48° C., the temperature range of the "heat" experience in question is evidently quite limited under ordinary conditions. (See Fig. 88.)

395. Thermal Experience as a Function of Spatial Factors. — An exploration of the skin with stimuli of very small area reveals two very significant facts, (1) that thermal experience can be evoked only from certain restricted and permanently localized spots on the cutaneous surface, and (2) that these thermal "spots" are specific for warmth and coolness, respectively. A "warm spot" never yields an experience of cool, and a "cool spot" never yields one of warm, no matter how they may be excited. The average number of cold spots per square centimeter is 12–13, while that of warm spots is 1–2. The exact number varies with the part of the body which is considered, and the distribution is irregular or statistical in character, within any small region. Sommer [616] estimates that there are 250,000 cold spots and 30,00 warm spots in the entire body surface.

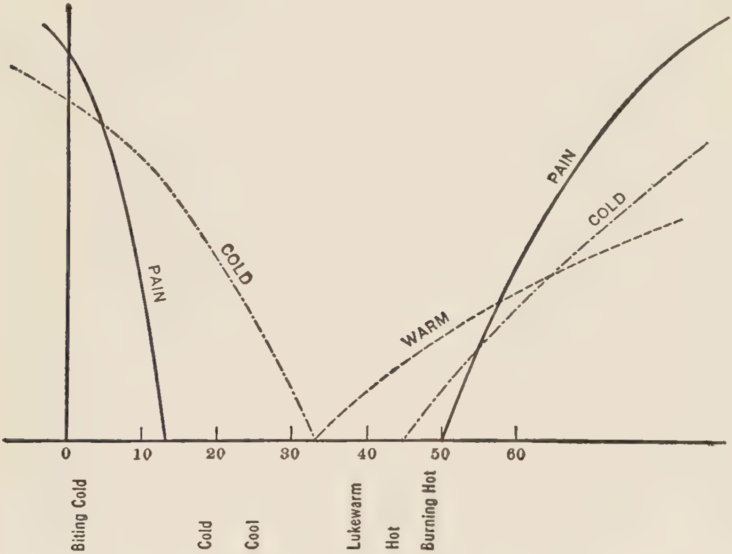


FIG. 88. THERMAL RESPONSES OF THE SKIN.

These curves, after von Frey, indicate the degrees of response of the thermal and pain systems of the skin at the temperatures, Centigrade, represented on the base-line. (*From Pillsbury: Fundamentals of Psychology, Macmillan.*)

There is no region of the body where the density of the warm spots is in excess of that of the cold spots, but there are some regions where both are absent, as in the case of the cornea of the eye. The glans penis, and the conjunctiva and sclera of the eye, are practically free from warmth spots, but possess cold spots. The interior of the alimentary canal, together with the viscera, are devoid of temperature sensibility, but thermal spots are found in abundance within the mouth, the nose, the anus, and the external auditory meatus. In general, the trunk is more sensitive to heat than are the extremities, and in regions where the tactile sensibility is high — as at the finger tips — the thermal spots have been crowded out to a considerable extent. Thus, the thermal sensibility of the right hand is less than that of the left.

We have seen that the magnitude of the threshold for thermal response varies with the location of the stimulus upon the body surface. Since the distribution of such thermal sensibility correlates closely with that of the density of warmth or cold spots, we may attribute its variations to this factor, although the thickness of the skin may play some part. In harmony with this view, experiment shows that the threshold decreases as the area of application of the stimulus is increased on any given section of the body surface. If the stimulus is above the threshold for a small area, the intensity of the warmth or cold experience will increase supraliminally with the area. In terms of thermal spots, the intensity and the reciprocal threshold are higher the larger the number that is stimulated in the same manner. Such areal summation is greater, the nearer the coexcited spots are to one another, and is absent when they are widely separated. When a cold spot and a warmth spot which are very close together are simultaneously excited, there may be a rapid alternation of non-spatially-separated cool and warmth experiences, a phenomeon resembling retinal rivalry.

In spite of the apparent antagonism between the warmth and the cold responses, there is no such effect as simultaneous thermal contrast.[617] Thermal sensations also show relatively little irradiation.

396. Thermal Experience as a Function of Temporal Aspects of the Stimulus. — *Reaction Times.* — Judging from reaction-time measurements, the interval between the application of the stimulus and the appearance of the thermal impression in consciousness, is greater in the case of warmth than in that of cold. Thus, using strong " in-tangible" stimuli, Tanzi[618] found reaction times of 0.227 seconds for cold, and 0.507 seconds for warmth; with tangible stimuli the corresponding times were 0.137 and 0.162 seconds, respectively. Weber[619] noted that the times required for the development of thermal impressions are greater, the thicker the skin in the region which is tested. Thermal experiences also show a marked tendency to persist after the external stimulus condition has been removed. This can be attributed, at least in part, to the considerable time which is required for the given portion of the skin to return to its normal temperature.

Adaptation.—Probably the most important temporal relationship of thermal sensation is its reduction in intensity with time, under constant objective stimulus conditions. The studies of Culler show that complete adaptation is possible only when the stimulus temperatures are close to normal skin temperature, and that the equilibrium thermal intensity is higher the greater the departure from this condition. Cold shows less reduction in intensity with time than does warmth, other conditions equal. The time required for equilibrium adaptation is approximately proportional to the difference between the given temperature and the normal skin temperature. The laws are evidently very similar to those which hold for either achromatic or chromatic vision.

As previously noted, thermal adaptation can be interpreted as a change in the physiological zero, thus implying a progressive alteration in the effective value of the stimulus. If such changes are not reversed, they demand that an adaptive decrease in the intensity of cold should be compensated by a corresponding increase in the intensity of warmth for any stimulus condition which is capable of evoking the latter; or *vice versa.* Skin temperatures which yield warmth under one state of adaptation may yield cold under another. These expectations are realized in the facts. Thus, if one hand is immersed in cold water and the other in warm water, and adaptation is allowed to proceed, water at normal skin temperature will then yield warmth from the first hand and coolness from the second. Here again the interrelations of thermal sensibilities show a close resemblance to those of opposed chromatic modalities in vision.

397. **The Identity of the Thermal End-bulbs.** — The skin contains a large number and variety of receptor organs, practically all of which are located in the true dermis, below the epidermis, so that the influence of the stimulus must be transmitted through the latter before it can act upon the end-organs. The receptors are distributed throughout the four principal layers of the dermis in a manner which is

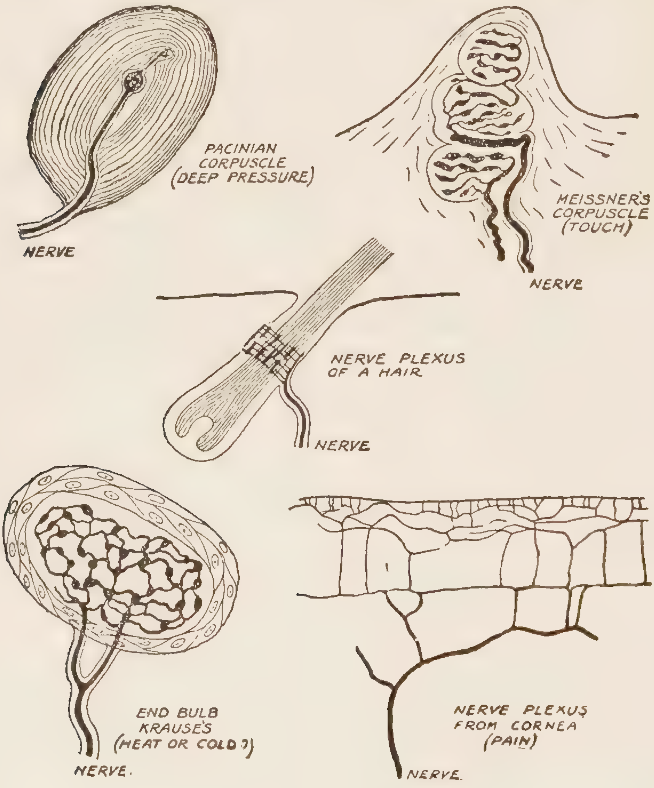

PACINIAN CORPUSCLE (DEEP PRESSURE)
NERVE
MEISSNER'S CORPUSCLE (TOUCH)
NERVE
NERVE PLEXUS OF A HAIR
NERVE
END BULB KRAUSE'S (HEAT OR COLD ?)
NERVE.
NERVE PLEXUS FROM CORNEA (PAIN)
NERVE.

FIG. 89. RECEPTORS OF THE SKIN.

Five different types of nerve end-organs, found in the human skin, are shown. (*From Starling: Principles of Physiology, Churchill.*)

more or less characteristic of the individual types. It is somewhat difficult, however, to classify the receptors definitely upon an anatomical basis, because of the manifold variations which led Ruffini to say that each tactile corpuscle requires individual description. Their physiological separation presents even greater difficulties, and the results thus far attained indicate that similar appearing receptors do not of necessity perform the same functions; and, conversely, that similar duties may be fulfilled by end-organs which are dissimilar histologically. The cutaneous receptors consist characteristically of a tangle of fibrous arborizations, which are enclosed in a capsule varying in its exact shape and complexity of laminated structure. The various typical forms have been named after the anatomists who have discovered or investigated them. As a rule, a considerable number of these end-organs are connected to the branches of a single cutaneous nerve fibre.

Since the points of specific sensibility for warmth and cold, on the skin, are separately localized, we should expect to find two different classes of receptors for these respective kinds of response. This expectation is strengthened by two other considerations, (1) that the receptor mechanisms which are required for reaction to increase and decrease of temperature, respectively, must naturally be different, and (2) that the latent period and reaction time for cold are much lower than for warmth. This latter consideration indicates that the receptors for warmth lie in a deeper stratum of the skin than do those for cold. The attempt to identify the specific receptors for these thermal responses is aided, furthermore, by the fact that certain areas of the body surface show no warmth reaction.

This is the case with the conjunctiva and sclera of the eye, and recent painstaking investigations by Strughold[620] make it quite clear that the so-called end-bulbs of Krause (see Fig. 90), are the operative receptors for cold in this region. Strughold succeeded in staining the end-bulbs in the living eye and in identifying their locations with those of the cold spots. The stain also produced an anaesthesia to cold when it acted upon the end-bulbs. These results confirm the previously expressed views of von Frey.[621] Structures similar to the organs of Krause are found in the glans penis and clitoris (where there is cold sensibility but no warmth sensibility) although their structure is somewhat more complex. Luciani [622] concludes that, by a process of elimination, we may assign the "cold" response of the skin to Dogiel's corpuscles, Ruffini's papillary endings, and the Golgi-Mazzoni corpuscles; while the Pacinian and Ruffinian corpuscles are responsible for the warmth sense. The latter group lie in the deeper layers of the skin, whereas the former are more superficial in their locations, corresponding with the characteristic differences in latent period between the two thermal modalities. The Pacinian bodies have a very typical structure, differing quite radically from that of the Krausian end-bulbs. The former consist of a single axis cylinder, thrust through an onion-like formation, to produce a straight core within the latter, with a little knot of fibrils inside the corpuscle at the end opposite to its stem. (See Fig. 89.) The cold receptors all have a complicated skein structure, enclosed in a relatively few layers of sheath tissue.

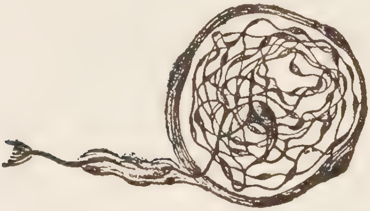


FIG. 90. KRAUSE END-BULB FROM THE HUMAN CONJUNCTIVA.

The investigations of Strughold show that these organs are the receptors for "cold" in the conjunctiva and sclera of the eye. The nerve-ending forms a globular skein encased in a delicate capsule of connective tissue.

398. **Hypotheses Regarding the Thermal Receptor Process.** — Our knowledge of the psychophysiology of the thermal response system is so inaccurate at the present time that hypotheses concerning the mechanisms of the end-organs cannot be adequately controlled by the data. It is quite easy, however, to construct such hypotheses which will fit the facts so far as they go. The theory which was advocated by Hering,[623] according to which "cold" and

"warmth" correspond with anabolic and catabolic process, respectively, in a single receptive substance is, of course, ruled out by the anatomical distinctness of the two response mechanisms. The function of the "warmth receptors" must be conceived as that of reacting to increases in skin temperature by generating a series of excitation pulses in the nerve fibres to which they are attached, or by increasing the pulse frequency, if excitation already exists. Owing to the fact that the thermal end-organs do not respond to mechanical stimuli, as well as to the high degree of adaptation which they manifest, it seems almost certain that their essential mechanism is chemical. The specific action of menthol on the cold receptors and of carbon dioxide on the warmth receptors corroborates this general conclusion.

The Case for Warmth. — Now, it is a familiar principle expressed in van t'Hoff's law, that chemical reactions tend to increase in velocity with increasing temperature. Hence we may suppose that the end-bulbs for warmth contain a chemical substance, *W*, which undergoes decomposition at a rate that increases as a function of the skin temperature. Some end-product, *W*, of this reaction may be supposed to act upon the nerve membrane so as to produce periodic depolarization in accordance with a mechanism similar to that which we have already discussed in Section 50, above. In accordance with the principles there outlined, the frequency of the nerve impulses will be determined by the concentration of *W*. However, an increase in the rate of decomposition will tend to exhaust the supply of *W*, so that the impulse frequency will soon decline, and will finally reach an equilibrium condition, representing a response which is lower in intensity than that which immediately followed the increase in skin temperature. This accounts for the general facts of adaptation, just as in the case of vision.

The Case for Cold. — It is much easier to account for response to temperature increase than to that to temperature decrease. We might, perhaps, endeavor to explain the stimulating action of cold in terms of some purely physical contraction, but the symmetry of the adaptational and threshold phenomena in the dual temperature response system indicates strongly that both forms of reaction belong in the same category, and may even have chemically identical components. We may therefore suppose that, in the case of the "cold receptors," we have to deal with a duplex chemical system, in which there are two decomposing substances, W and X, the second being relatively insensitive to temperature change (having a low temperature coefficient). The first substance may be the same as that which operates in the "warmth receptors" and has a high degree of thermal sensitivity. We may furthermore suppose that the end-products of the X reaction are responsible, now, for the nerve excitation and that those of the W reaction neutralize them or render them ineffective, quantitatively. Hence, a temperature decrease should bring about an increase in the nerve pulse frequency, by increasing the amount of unneutralized X substance. Adaptation is to be attributed to an accumulation of W, which finally increases the W reaction again, in accordance with the principles of mass action.

Relations of Warmth and Cold Response. — This system readily permits us to account, in a qualitative manner, for the functional symmetry of the temperature response system, its adaptation characteristics, and also for the existence of the paradoxical cold reaction. Temperatures as high as 45° C. may very well augment the velocity of the X reaction to such an extent that it can no longer be neutralized by the concomitant W reaction, or its products. It is quite reasonable to suppose that the W reaction will fail to maintain its characteristic functional relationships to the X reaction, at high temperatures, in consequence of its high thermal sensibility. The correspondence between the two processes may be compared to that between the proportions of retinal rod and cone response at various intensity levels, the rod response being quite submerged by that of the cones at high illumination although at lower levels the rods are predominant.

The antagonism which evidently exists between the warmth and cold responses must be attributed to the way in which the respective nerve currents influence each other in the synaptic regions of the spinal cord or brain. Apparently, the connections at these points are such as to cause equal neural intensities in the two channels to cancel each other, in accordance with a law of the form:

$$N = H - C$$

When N is positive, the experiential quality is "warm" and when it is negative, the quality is "cold." The two nerve processes inhibit each other, but the amount of inhibition cannot exceed that of the process which is the weakest. The inhibition is complete only when both currents are equal. The theory which we have outlined above suggests that the warmth and cold receptors will always be delivering streams of nerve pulses to the centers, even at normal skin temperature and equilibrium adaptation, but under these conditions the opposed nerve processes will be equal and hence mutually annihilative.

399. Neurological Correlations of Thermal Experience. — No general difficulties, such as those encountered in the cases of vision, audition, and olfaction, are found in imagining how thermal "signals" are transmitted from the receptors to the cortex, so as to determine the corresponding experiences. We may suppose that the degree of excitation of the cold or warmth paths consists in the number of quantal nerve pulses per second along a unit group of conductors. The intensity of the thermal experience must be a direct function of this impulse density. The unit fibre group may be rather large, accounting for areal summation, although this may also be attributed, to some extent, to the fact that numerous receptors are attached to a single conductor. Pressure on the ulnar nerve trunk at the elbow brings out temperature experiences localized mainly on the ulnar section of the hand.

The qualitative distinction between warmth and cold must be supposed to rest upon the topographical separateness of the two classes of nerve paths, the cortical termini of these paths being specifically differentiated as to substance. The mutual inhibitory influence of the two classes of currents upon each other must be such as not to involve any coalescence between them, but to be restricted to a purely interactive relationship in which a unit pulse in one path cancels a unit pulse in an associated path of opposite kind. The effectiveness of this cancellation must be a function of the degree of proximity of the two paths, being most marked within the domain of a "unit fibre group." [624] Under some conditions, such as that of the paradoxical cold reaction and the evocation of the experience, "hot," there is some degree of break-down of this neural interference even within a single fibre group.

Section 69

TACTUAL SENSATION

Tactual experience presents a very homogeneous group of qualities, at various intensities, which are correlated with certain distributions of pressure upon the body surface. (See Note E or Volume I.) In order to secure this kind of experience in pure form, there must be no appreciable interference with thermal exchanges or injury to the skin. The two characteristic qualities are tickle and touch (or pressure feeling), each of these being capable of existing at a number of different intensities, in graded series.

400. The Nature of the Tactual Stimulus. — We have seen that the objective precondition for tactual quality consists in the establishment of sufficiently high pressure gradients along the cutaneous surface. The immediate effect of such gradients consists in the distortion or deformation of the skin, and such deformation transmits pressure gradients to internal tissue layers. Thus, the condition for the arousal of touch may be either a change in form of the individual receptors or a difference in pressure upon adjacent, neurologically separable, receptors. These principles seem to apply equally, whether touch is elicited by the deflection of a hair or by pressing upon a restricted region of hairless skin surface. The movement of the hair is transmitted to its root and produces a deformation of the surrounding tissues, which contain the receptors.

Von Frey[625] showed that touch is aroused as readily through deformation of the skin by traction as by pressure. He cemented a disk to the skin and then pulled upon it, and found that the force which was required to yield threshold response was practically the same as when pressure was applied to the same area. Tactual response can also be evoked or reinforced by the local application of cold to the skin, this effect being attributable to local shrinkage of the tissues in consequence of circulatory reactions, or possibly to some extent of a purely physical contraction.

401. Tactual Quality and Intensity as Functions of Stimulus Magnitude. — The fact that the tactual stimulus consists in a pressure gradient, or rate of change of pressure with respect to position, makes it difficult to separate the intensive from the extensive characteristics of the stimulus in question. Theoretically, it might be possible to deal with the gradient values at mathematical points on the skin, but it is doubtful whether such values would have any real significance. In experiments dealing with the determination of tactual experience by pressure distributions, it is common to maintain constant the area of action of the external object upon the skin, while the force acting through this area is varied. Under these conditions the pressure (force per unit area) and the pressure gradients will change more or less in proportion to the values of the applied force. If we use the smallest possible area, the pressures and gradients will be maximal for the given amounts of force.

Experimenting in this way, we find that the *tickle quality* is evoked by light pressures, particularly when these are narrowly localized upon the skin surface. Thus the quality which is elicited by the deflection of individual hairs is ticklish, and must be conceived to involve a relatively slight tissue distortion within a very small area or volume, only a single receptive unit probably being involved. Touching a portion of the skin directly with an object such as a feather, which applies very light pressures to small areas, yields a qualitatively similar experience. As we shall see later, the time of action is also a factor in determining the ticklish quality.

When the area of action is larger, and the pressure gradients are higher, the touch quality, proper, supervenes. As we have already noted, Hensen[626] found that an increase of pressure of less than 0.001 gram, on a very small area of the skin of the face, yielded a definite tactual experience. Measurements by von Frey,[627] using contact surfaces varying between 1/16th to 1/500th of a square millimeter in area, gave pressure thresholds ranging from 2.0 grams per square millimeter, for the tongue and nose, to 48.0 grams for the loins. The finger-tips required 3.0 grams per square millimeter, and the back of the hand 12.0 grams, for the same area. Probably the most sensitive end-organs for touch are the hairs. It has been found that the threshold for touch on a given area of the skin may increase by a factor as great as 18 when it is shaved. The force required to stimulate the most sensitive touch spots in the region near a short hair is from three to twelve times that which must be applied to the hair itself.

When stimuli of considerable area are employed, it is found that the just noticeable increase in touch intensity, above the absolute threshold, corresponds to a constant fractional increase in the force which is applied to the skin, provided the forces are of medium magnitude. In other words, position in a psychological scale of tactual intensities varies as the logarithm of the pressure, for constant area. The first demonstration of this relationship was made by Weber[628] himself for such tactual values. The required fractional change is a function of the region of the skin which is tested, being from 1/40th to 1/30th for the skin of the face, 1/20th to 1/10th for the hands and fingers, and greater than 1/10th for the skin of the legs and feet. As in other senses, the relationship breaks down at very low and very high stimulus intensities, where the required fractional increment is greater than in the medium intensity range. Schriever [629] finds that Weber's law holds for tactual stimuli of minimal area, if suitable constants are employed in plotting the relationship between the intensity and the just noticeable difference in intensity.

402. Tactual Intensity as a Function of Stimulus Area. — Exploration of the skin with pressure stimuli of very small area, such as fibres of glass wool, shows that the sensibility for touch is restricted — like that for warmth and cold — to definitely localizable spots, with quite insensitive intervening regions. The average number of such "touch spots" per square centimeter is about 25, but their density is said to vary by factors of about 1 to 6 for different parts of the body although, according to Titchener,[630] there are 300 per square centimeter on the scalp. Careful studies by Kiesow [631] have shown that the absolute thresholds for the individual spots are highly variable in any single general location, and also that the average threshold for a collection of spots is a function of position on the body surface. Thus, the average threshold for the touch spots in the median line of the back is about seven and one-half times that of the spots on the forehead. The lowest individual thresholds, however, show a much greater range of variation, those for the tip of the tongue being about one-twentieth those for the finger tips of the left hand.

The distribution of spots over the body surface is in part such as to compensate for such differences in sensitivity, by providing more spots where the average threshold is higher, and in part such as to augment the inequality. Thus, the forearm has few spots but comparatively high sensibility, whereas the middle of the back is deficient in both respects. In general, those portions of the body which have the greatest motility also have the greatest number of touch spots and the highest general sensibility. Certain bodily areas are found to be quite free from touch spots. These areas include the corneas of the eyes, the conjunctivas of the upper eyelids, and the inner lining of the alimentary canal. The internal organs show no tactual sensibility, but touch spots are found in abundance in the membranes of both extremities of the alimentary canal. The tongue is the most sensitive of all tactual organs.

The experiments of Kiesow[632] show that an increase in the area of application of a tactual stimulus, not only requires increased force but also increased pressure, or force per unit area. This is to be attributed to the fact that an effective pressure gradient is created only at the edges of the area which is acted upon, so that the force which is exerted upon internal elements of surface is deprived of stimulating value. Consequently, Kiesow's observations do not necessarily mean that there is no summation of influence between adjacent sensitive points, when they are actually stimulated.

403. Tactual Quality and Intensity as Functions of Temporal Aspects of the Stimulus. — *Tickle.* — We have already noted that the ticklish quality of touch tends to go with weak stimulation of small areas of the skin. Its evocation is also favored by maximally brief action of the stimulus. Thus, if the hairs of the back of the hand are brushed over quickly, the quality of the resulting experience is more ticklish than when the contact with individual hairs is prolonged. The hairless skin surfaces respond in the same manner.

The *latent period and reaction time* for touch are slightly briefer than those for cold, being considerably shorter than for warmth and much shorter than for pain.

"Vibration Sense." — Stimulation of the skin with a vibrating body, such as a tuning-fork prong, yields an impression of roughness or vibration up to frequencies of 2600 per second. According to Gault,[633] differences in frequency can be discriminated by touch with an accuracy of 9 percent, and particular vibrational forms, such as those of vowels, consonants, etc., can be recognized, with practice. At frequencies higher than 2600, the impression is one of smooth contact.

Positive After-Effects. — Although the rate of decay of the individual touch impression is thus quite rapid, nevertheless, persistent positive after-effects are common. In some cases, such effects can be attributed to a continuing distortion of the skin, but in other instances this explanation hardly seems applicable. The conditions which favor tickle also yield persistence, and these can cause no enduring indentation of the skin. The determining factors are probably to be found in the central nervous system. Strong positive tactual after-images are frequently a symptom of general nervous fatigue or exhaustion.

Adaptation.—The tactile sense also exhibits a considerable amount of adaptation. The intensity of the touch experience decreases progressively with time, when the stimulus conditions remain constant, but the process is much less rapid and complete than in the case of the thermal sense. When the stimuli are close to the absolute threshold, the corresponding touch experiences readily vanish, but when they are at higher levels the tactual response may persist for hours. Eventually, as in the case of spectacles or eyeglasses, the corresponding tactual experiences may wholly disappear.[634] Von Frey and Kiesow[635] found that the rate of application of a tactual stimulus has an important bearing upon its effectiveness, slow application raising the threshold. This effect can evidently be attributed to adaptation, as in the case of the temperature sense.

404. Composite Tactual Sensation.—In the Section dealing with composite tactual perception (Volume I), we have considered the manner in which the structure and localization of tactual experiences depends upon that of objects in contact with the skin. The facts, there presented, can readily be translated into corresponding sensory terms, by replacing the objective factors with the related stimulus aspects. In terms of the tactual stimulus, it appears that the structure of experience is determined by the distribution of pressures upon or within the skin. However, the relations of such distributions to the locations of touch spots are of considerable importance. It is found that when local pressures are registered accurately with the touch spots the two-point limen is usually considerably reduced. This is to be attributed to the greater confinement of the stimulus action to individual receptive points.

405. The Correlations of Experience and the Tactual Receptor Process. — *The Receptors.* — The restriction, or centralization, of tactual sensitivity about the so-called touch spots indicates the positions of the tactile receptors. Available evidence tends to identify the latter with the nerve coils at the roots of the hairs and the so-called Meissner's corpuscles in the hairless regions of the body. These corpuscles exist in many different varieties, but typically have a structure such as that represented in Fig. 89. They comprise loops and coils of nerve arborizations, enclosed in a homogeneous central tissue, which is surrounded by a relatively light laminated envelope. The distribution of these corpuscles in the body surface is similar quantitatively to that of tactual sensibility. Their position in the superficial layers of the dermis corresponds with the relatively low threshold and sharply punctate character of tactual response; and harmonizes well with the accessibility of touch to electrical stimulation and its disappearance in cutaneous scars. However, it is likely that other end-organs are also concerned in touch, especially for heavy pressures.

The functions of the tactile corpuscles must undoubtedly be, firstly, to increase the sensitiveness of the nerve-ends to pressure stimuli and, secondly, to permit the generation of a more or less persistent series of nerve pulses. A bare nerve fibre can be stimulated by impact, but it has been shown by Tigerstedt[636] that the minimal mechanical stimulus under such conditions consists in a mass of 0.2 grams, moving at 140.0 millimeters a second; while for a touch spot, von Frey found that the same mass, moving at 0.17 millimeters per second was sufficient. This amounts to a factor of 820 in speed, or of about 670,000 in kinetic energy! The experimental observations of Adrian and Zotterman[637] have shown that the deflection of a cutaneous hair results in a series of all-or-none pulses in the corresponding cutaneous nerve. Similar consequences follow from pressure upon the skin. When the pressure is very light, there is merely a momentary burst of impulses, but when it is heavy, the current is more persistent. Direct mechanical stimulation of a nerve does not ordinarily produce a series of impulses in this way.

The Operation of the Pressure Gradient.—The fact that touch shows a very considerable degree of adaptation, particularly for weak stimuli, suggests that the receptors are equipped with a chemical mechanism which is sensitive to pressure or pressure gradient. It is well known that the velocities of chemical reactions are affected by pressure. A pressure gradient, however, can bring about a bodily transfer of substance from one point to another, and such movement of material may be the condition for localized chemical reactions, or changes in ionic concentrations, which may bring about excitation. The seeming requirement of a pressure gradient for tactual stimulation can be interpreted in a number of different ways. The gradient, or pressure difference, may be needed either (1) to operate the individual receptors, or (2) to elevate the excitations of such receptors above that of the general mass of receptors. Under the first alternative, it seems rather doubtful whether a pressure gradient must be established throughout the volume of the individual tactile corpuscles, because they are most adequately stimulated when pressure is applied centrally over their individual loci. However, with such conditions, the pressure is radically different in different directions, being maximal vertically and less in the plane of the skin. This distribution of forces would tend to flatten the corpuscle, whereas a wider distribution of uniform pressure on the skin surface would yield forces about the receptors which are less variable as functions of angle with the cutaneous surface.

Under the second alternative, above, we may recall Fechner's belief [638] that the entire system of tactual receptors is subject to a self-excitatory action which lies at the basis of a permanent perception of the total tactual field. Yet contact with particular skin points yields experiences which are distinct from the field as such. Hence we should have to suppose, on the Fechnerian assumption, that a *difference* in excitation between adjacent neuro-receptoral units is required in order to evoke a distinctive tactual impression in consciousness. Such a supposition would permit us to assume the receptors to be sensitive to pressure, *per se;* a pressure gradient would be needed to yield an outstanding tactual quality only to overcome a neurological cancelling action of adjacent excitations upon one another. This doctrine would seem to imply that all tactual experience, apart from that of the empty touch field, represents boundary conditions.

Tickle. — It is evident that the intensity of the tactual stimulus must be a function of the magnitude of the concurrent chemical or osmotic changes within the receptors, increasing directly as the magnitude in question. The basis for the difference between tickle and touch would appear to lie in the temporal and spatial patterns of the two excitations, tickle being evoked when the process is restricted to a small number of receptors and to a brief interval of time, whereas touch goes with a more extensive and persistent excitation. Tickle would belong in the class of "phasic" (momentary) and touch in that of "postural" (relatively persistent) sensory response.[639] It is possible, however, that there is a selection between separate classes of tactile end-organs, such as protopathic versus epicritic, on the ground of stimulus intensity difference, the tickle organs lying more superficially in the skin and being excited phasically by pressure changes which distort the tissues only slightly, while the more "postural" tactual receptors are aroused only by pressures which penetrate more deeply.

The neurological basis of the areal and temporal structures of tactual experience may best be considered in connection with the psychophysiological correlations of the afferent nerve processes, below.

406. Tactual Experience as a Function of the Afferent Nerve Currents. — The studies of Adrian,[640] as well as the general demands of the all-or-none principle, make it evident that the intensity of tactual sensation is a function of the rate of arrival of quantal nerve pulses at any cross-section of a small group of affiliated tactile fibres. This quantity can also be designated as the *total impulse frequency* for the group in question, or as the volumic impulse density. The tickle quality may be assigned to clusters of impulses which are restricted to a few fibres, possibly to a single one, and of brief duration. Nerve currents of this sort have been noted by Adrian in conjunction with excitation of the hairs, or of very light touches upon the toe-pad, in the case of the cat.

Spatial Configurations.—The pattern of the tactual experience is determined by the distribution of neural quanta over the entire system of afferent tactile nerves, at any given time. It might seem, perhaps, that doubleness of impression, in the case of the two-point limen, should depend upon the excitation of two adjacent nerve fibres, as compared with that of only a single fibre. It is well known that a number of individual receptor organs are attached to a single afferent conductor, but in the case of the touch corpuscles, this number usually does not exceed four or five; and examination of the data shows that a tactual "sensory circle" may embrace more than 200 touch spots. Moreover, on account of the interweaving distribution of the receptive branches of two adjacent cutaneous nerve fibres, we should expect the magnitude of the sensory circle to be very variable in any one general region of the skin, if the condition for doubleness lies in the simultaneous innervation of only two fibres. Similar results should also be expected even if the receptors belonging to single nerves were rigorously segregated. Hence we must adopt some such view as that of Bernstein (*cf.* Volume III), which looks to the cerebral cortex for the factors that essentially determine the two-point limen, and supposes that a considerable number of adjacent fibres are involved in the experience of single tactual points. The fact that the limen can be radically reduced by practice favors such a view.

With regard to the part which is played by the afferent fibres, we can only say that the limen cannot conceivably involve less than two distinct nerve channels, regardless of the number of individual receptors which may be concerned. As in the visual case, we may think of a unit number of co-operating fibres, the processes of which combine to yield an intensive, rather than an extensive, result in consciousness. But when the extent of the stimulation exceeds the confines of this group, the intensity increase gradually gives way to an extensity effect. If we think in terms of such fibre groups, the constellation of excitations among them must be regarded as determinative of the pattern of the tactual experience in consciousness, both intensively and extensively. *Localization* obviously follows the same general principles as does pattern, implying only some sort of effectiveness of the entire system of tactual or cutaneous conductors, with respect to consciousness, whether or not they are actively excited. The exact organization of the touch field in relation to consciousness must rest upon central nerve connections. It is in the centers, therefore, that we must look for the explanation of such phenomena as Aristotle's illusion. (*Cf.* Volume I.) However, given any particular set-up of the central connections, the result is determined by the distribution of excitation among the afferent channels.

Temporal Patterns. — The temporal course of tactual experience will naturally be referred to the corresponding course of the receptoral and nerve conductional process. The so-called vibrational sense seems to present a dilemma, due to the fact that the tactile nerve currents are always of a definite pulsatory character, without uniformly yielding any corresponding intermittency of feeling (except possibly in the case of tickle). The resolution of this difficulty is probably as follows. In ordinary tactual response, the flow of impulses, as shown by Adrian's studies upon multifibral preparations,[641] is highly irregular, so that no constant periodicity is impressed upon the receiving cells in the cerebral cortex. However, when a vibrating stimulus is employed, a considerable number of receptors are excited in synchronism, so that a regularity of impulse transmission is impressed, not only upon individual fibres, but upon a large number of fibres conducting in parallel. This is sufficient to produce an appreciable periodicity in the central process. Thunberg[642] and others have questioned the possibility of the tactile nerve transmitting frequencies as high as 2600, or even 1552, the older figure. Although present estimates of refractory period do not put such transmission entirely out of the question, nevertheless, we may be forced to appeal to the same principle which has been employed in the case of audition. The studies of Adrian[643] show that it is quite common for frequencies to exist in a multifibral nerve preparation which are higher than those which are possible for the individual fibres; and the work of von Frey[644] has demonstrated that the tactual end-organs are capable of the summation of subliminal intensities, so that if they are not excited by the first impact they may respond at a subsequent one. Under these conditions, it would be natural to suppose that frequencies higher than those which can be transmitted by a single nerve fibre can be carried by a *group* of conductors, and yet stand in a constant temporal relationship to the vibrations of the stimulus.

The various qualitative "modes of appearance," "modifications," etc., which have been signalized in the researches of Katz (see Volume I), must be attributed to variations in the concurrent temporal and spatial patterns of the afferent nerve impulses, within the tactile field. The central conditions for some of these phenomena will be discussed in greater detail in Volume III.

Section 70

CUTANEOUS PAIN SENSATION

From the introspective standpoint, there is a sharp qualitative difference between touch and pain, even if we disregard the usual unpleasantness of the latter. (See Note E and Volume I.) It is, of course, necessary to avoid any confusion between the concept of pain, or algesic quality, and negative affection or unpleasantness. Any experiential quality whatsoever may be unpleasant, and although pain is commonly very unpleasant it is frequently indifferently affective, and in the case of "itch" may even be decidedly pleasant. On the other hand, cutaneous pain, considered quite apart from its affective aspects, is of course only one species of algesic quality. There are many varieties and conditions of the latter, and some of these in addition to the cutaneous pains will be considered in our discussion of organic sensation in a subsequent section.

407. The Pain Stimulus. — As Sherrington[645] points out, the pain receptors appear to be responsive to a variety of different stimuli, being to this extent non-selective in contrast to the normal selectivity of special sense-organs. However, all of these stimuli, at the intensities where they affect the algesic sense, have the common aspect of injuring or of threatening injury to the skin, and possibly to the nerve tissues, themselves. As we have already noted, pain can be evoked by chemical action, extreme heat or "cold," electrical voltage, as well as by mechanical forces which seriously indent or lacerate the dermis. Pflüger[646] has noted that the temperature (48° C.) at which cutaneous pain appears, coincides with that at which the nerve substance begins to be damaged by the heat. In the case of mechanical forces, the tendency to excite pain increases rapidly with the degree of spatial restriction of the action, with the accompanying increased tendency to cleave the skin. This means that a pressure gradient is required, as in the case of touch, but this aspect of the pain stimulus is even more marked than in the case of the tactual one. Thus, according to von Frey,[647] for areas of action lying between 3 and 12 square millimeters, pain requires a thousand times more force than does touch, but with the smallest possible areas of application, the required forces for threshold excitation may actually be lower than those for touch. This latter comparison also holds for electrical voltages.

408. Algesic Experience as a Function of Stimulus Magnitudes. — No quantitative data seem to be available concerning the evocation of pain by chemical stimuli. As already noted, pain results from temperatures below about 12° C. and above 48° C. The mode of variation of pain intensity outside of these limits, as a function of temperature, is unknown, but its regional distribution has been studied by Goldscheider.[648] Bernhardt [649] has made comparisons of the pain thresholds of different portions of the body, for electrical stimuli, and naturally finds the values to be higher in the regions which are thick-skinned, than in those which have more delicate tissues.

When mechanical stimuli are employed, the ratio between the touch and the pain thresholds has been found to vary from 1/3 in the case of the fore-arm to 1/100 for the finger tips. The intensities of the supraliminal pains which are evoked by mechanical stimuli of similar magnitudes are found to be greater in those portions of the body where this ratio is low than where it is high. However, no quantitative data appear to be available concerning the law of variation of algesic intensity with respect to the magnitude of the stimulus. We cannot say whether or not it follows Weber's law. At low intensities of excitation, particularly with minute areas of application, the quality of the experience changes to that designated as *itch.* This quality appears to sustain a relation to pain which is analogous to that which obtains between tickle and touch. It is well-known to be characteristic of moderate inflammatory conditions of the skin, such as those produced by insect bites. In this case, we probably have to deal with a weak chemical excitation of the algesic response.

A study of the distribution of pain sensibility over the skin shows that it is actually restricted to definite "pain spots," after the fashion of the thermal and tactile sensibilities. The average number of pain spots per square centimeter is about 175 on the hairy surfaces and 54 elsewhere (Strughold), although they are entirely absent in certain regions, particularly inside of the cheeks, opposite the second molar teeth. The total number of pain spots on the human body surface is said to be three and a half million. The variation in algesic sensitivity between different portions of the body is referable not only to variations in the areal density of the pain spots but also to differences in the local thickness of the epidermis. Identification of the pain spots is favored by epidermal thinness or flexibility, the latter property being improved in experimental studies by wetting the skin. Strong pressure upon a touch spot fails entirely to elicit pain, so long as adjacent pain spots are not involved.

409. Temporal Correlations of Pain. — The latent period and reaction times for pain are much higher than are those for touch. The former period is in the vicinity of 0.9 seconds, as compared with about 0.2 for touch. It is readily noted that when a portion of the skin is acted upon by a sudden intense force the touch precedes the pain in consciousness. When the pain is of high intensity it completely masks the characteristic tactual or thermal qualities, as soon as it has had time to develop. Intermittent electrical stimuli evoke an interrupted pain up to frequencies of about 20 shocks per second, above which a steady pain is experienced. Touch shows intermittency under similar excitation, up to 130 per second.

410. Composite Algesic Sensation. — There is a strong tendency for pain to irradiate over the experiential spatial field, filling an area which is much larger than that which corresponds to the cutaneous region which is acted upon by the stimulus. The experience is localized with fair exactness, following principles which are similar to those for touch.

411. Algesic Experience as a Function of Receptoral and Neural Factors. — *Action of the Free Nerve-Ends.* — It is quite definitely established that the receptive organs for cutaneous pain consist in the so-called free nerve-endings with which the skin and sensitive mucous membranes are profusely supplied. These endings ordinarily consist in a more or less complicated arborization of fibre branches. The cornea of the eye contains only such free nerve-endings together with Krause end-bulbs, and has been shown to be sensitive for pain and cold alone. Since the end-bulbs have been shown to belong to the cold sense, the free nerve-ends seem to be definitely assigned to pain. (See Fig. 91.)

The conditions of excitation of the pain sense resemble those for plain nerve tissue in that a rather wide variety of agencies are effective. The sensitivity to electrical action also suggests the response of plain nerve tissue. However, the pain thresholds are generally lower for the electrical stimuli than is the case for neural conductors in general, so that it is at least necessary to suppose that the nerve-ends are rendered specially sensitive. But there is one serious difficulty to be met in this line of reasoning, namely, the fact that the pain nerves respond with an especially persistent sensation. Adrian[650] has shown that there is a parallel persistence, or lack of adaptation, in the corresponding nerve currents. Such response is impossible for an unspecialized nerve cell, with respect to any of the stimuli which arouse the pain end-organs. It is therefore necessary to suppose that the so-called free nerve-ends of the skin are differentiated so as to be relatively non-adaptive as compared with conductional tissue, and presumably so as to have a much longer refractory period than have the essentially conducting sections of the fibres. The extremely long latent period and protracted after-effects of the pain sense suggest that the processes of the nerve-ends have been slowed down to an extreme degree. This feature may well be associated with the loss of adaptive compensation against the action of the stimulus, which is so characteristic of conducting fibres.

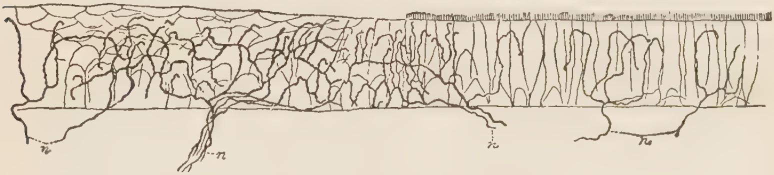


FIG. 91. FREE NERVE ENDINGS.

This figure shows the distribution of intra-epithelial nerve terminations in the larynx. The sensory nerve channels are designated by the letter, *n*. (*From Bayliss: Principles of General Physiology; Longmans, Green & Co.*)

In considering the correlations of algesic experience with the characteristics of the corresponding afferent nerve currents, we shall probably have to deal with unit groups of fibres, each of which is related to an indivisible aspect of the experience. The intensity of the pain experience will increase as a function of the frequency of quantal impulses passing along this unit group of conductors. Clusters or bursts of relatively few impulses, distributed sporadically over the pain conductors, may be responsible for the quality known as *itch,* while relatively continuous impulse streams yield ordinary pain. Localization will depend upon the distribution of the currents among separate fibre groups. We may suppose that the number of fibres involved in the evocation of a single pain point in consciousness is much larger than that which characterizes the sense of touch. The view, so elaborately developed by Goldscheider,[651] according to which pain accompanies high intensity of nerve conduction along any afferent channel, can now be rejected as without foundation.

Spinal Paths for Pain.—Great interest attaches to the fact that the paths followed by the pain impulses along the spinal cord are definitely separated from those taken by the currents for the other cutaneous modalities. This segregation, of course, makes it possible for the pain sense to be independently affected by pathological lesions. The pain impulses are carried in the lateral columns of the cord and are led to a special center in the thalamus. It is found that in certain stages of degeneration in the pain tracts, all normal pain stimuli elicit itch rather than pain — an observation which strengthens the interpretation of this quality as being determined by weak or irregular currents in the pain channels. Complete destruction or interruption of the pain tracts naturally establishes a condition of total analgesia for the regions of the body supplied by the nerve paths which are affected. This may occur without any change in the tactual or thermal sensibilities. We shall consider some of these central features of the pain system in further detail in Volume III.

Chapter XVIII

Kinaesthetic and Internal Sensation

Section 71

ABSOLUTE KINAESTHETIC SENSATION

We have seen in our discussion of absolute kinaesthetic perception (Volume I) that experience contains features which are correlated with the orientation, and the changes in orientation, of the body in space. Experiments show that these correlations apply more rigorously to the head than they do to the body as a whole, a fact which leads us to suppose that the receptors which are involved are located in the cranium. The loss of orientative sense which occurs in conjunction with deaf-mutism indicates the inner ear as the exact locus of the sense-organs in question. Here, in fact, we do find an elaborate apparatus which has no evident auditory function, but which is ideally constructed to subserve the requirements of a spatial sense. It has been shown that about fifty percent of all deaf-mutes have defects in this apparatus, as well as in that of audition, and this proportion agrees with that of the number of these unfortunates who have a defective kinaesthetic response. We may now consider how absolute kinaesthetic experience is related to the stimulation and response of the sensory mechanisms in question.

412. The Stimuli to Absolute Proprioceptive Response. — The stimuli to the proprioceptive systems of the inner ear are somewhat unique, in that no special mechanisms are required to transmit them from the environment to the sense-organ. In harmony with what we have learned in the chapters on absolute kinaesthetic perception, we can identify the stimuli with accelerative or gravitational vectors, operating upon and within the head. The action of these forces is dependent upon the masses of the parts of which the sense-organ is composed, these parts being displaced with respect to one another in directions which are determined by the directionalities of the forces themselves. As we have already seen, the latter can be divided into linear and rotatory types, and either of these can be resolved into components along three mutually perpendicular lines or planes. The gravitational force is of the linear type, whereas the rotatory vectors develop from spinning motions of the head or the body. (See Volume I.)

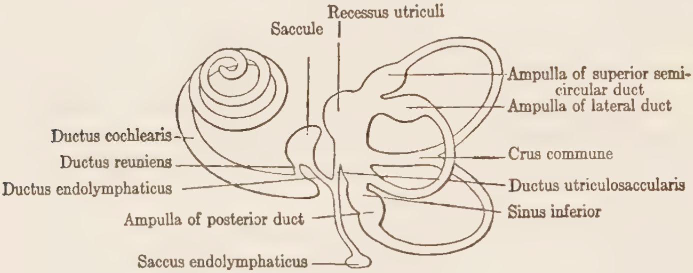

Recessus utriculi
Saccule
Ampulla of superior semicircular duct
Ampulla of lateral duct
Ductus cochlearis
Ductus reuniens
Crus commune
Ductus endolymphaticus
Ductus utriculosaccularis
Sinus inferior
Ampulla of posterior duct
Saccus endolymphaticus

FIG. 92. STRUCTURE OF THE MEMBRANOUS LABYRINTH.

This is a diagrammatic representation of the membranous portion of the inner ear mechanism. The parts which are concerned in the equilibrium sense are at the right, the coiled structure at the left being the cochlea or auditory organ. (*From Cunningham's Anatomy.*)

413. The Proprioceptive Sense-Organs of the Inner Ear. — The sensory apparatus in divisible into two functionally and anatomically distinct systems: the semicircular canals and the vestibular organs. The latter include the utriculus and the sacculus. The general structure and relationships of these parts are shown in Figs. 92 and 93.

The Semicircular Canals. — As represented in the figure, the semicircular canals consist of three arc-shaped tubes, which are disposed in three mutually perpendicular planes of space. One of these planes is horizontal, and the two vertical planes make angles of approximately forty-five degrees with the sagittal plane of the head, their intersections being in the mesial direction. The apparatus, of course, exists in duplicate on the two sides of the head, and the anterior canal on one side has the same directionality as the posterior one on the opposite side, so that the canals, as thus paired, presumably have corresponding connections with the central nervous system. The two horizontal canals must also be regarded as being similar to each other in function.

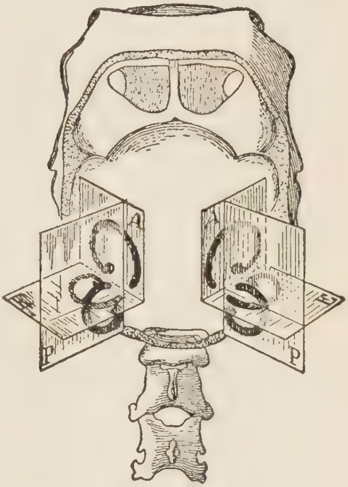


FIG. 93.
RELATIONSHIPS OF
THE SEMICIRCULAR CANALS.

This figure shows that the anterior canal on one side of the head operates in the same plane of space as the posterior canal on the other side. Both of the external canals are evidently in the same (or horizontal) plane. The sketch, by Ewald, is specifically for the head of a pigeon, but the relationships are the same as in the human case.

The three canals debouch into the utriculus at both ends, and the entire cavity is filled with a watery fluid which is known as endolymph. At one extremity of each canal, there is an enlargement, called an ampulla, which contains a sensory mechanism known as the *crista acoustica.* A cross-section of one of these is shown in Fig. 94. It consists of an elevation which bears radiating sensory cells equipped with long hairs, projecting into the cavity of the ampulla. These hairs support a rounded gelatinous mass, which mats them together, so that they tend to be displaced as a group rather than individually. The receptor cells connect with conducting nerve fibres which belong to the vestibular branch of the eighth cranial nerve.

The Utriculus and Sacculus. — The utriculus and sacculus each comprises a more or less ovoid sack, filled with endolymph. The former, as we have noted, is continuous with the semicircular canals, while the latter unites with the cochlear canal. However, it also joins the utriculus through a narrow passageway. Both the utriculus and the sacculus contain sensory structures which resemble those of the semicircular canal ampullae, but the hairs are embedded in a rather more dense mucous mass which carries particles of calcium carbonate, the otoliths. The area over which the receptor cells are spread is also considerably greater than in the case of the cristae acousticae. These organs are known as *maculae acousticae.* According to Titchener[652] the maculae of the utriculus and of the sacculus are disposed

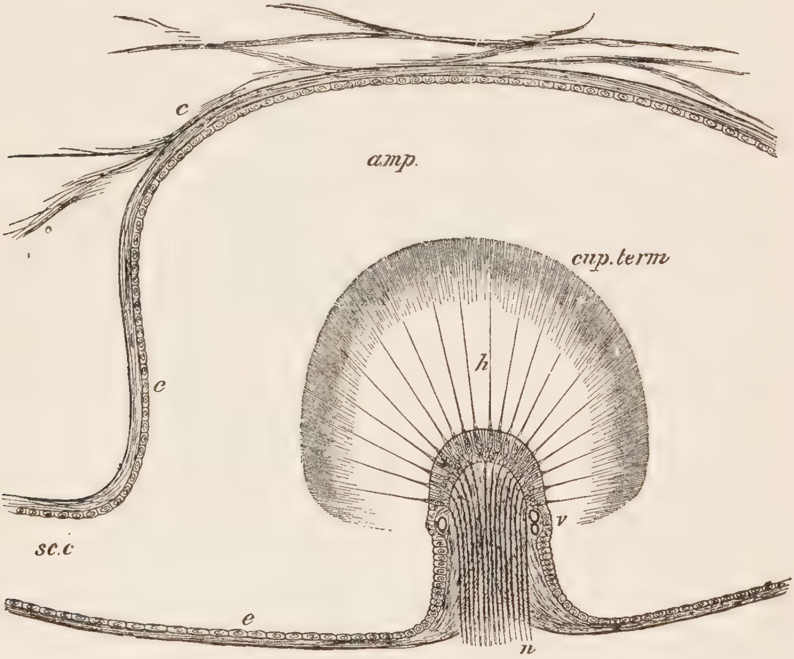


FIG. 94. AMPULLA AND CRISTA ACUSTICA.

This a longitudinal section of the ampulla of a fish, taken through the crista acustica. At *h* are seen the sensitive hairs, while at *n* are represented the afferent nerve fibres. The end of the semicircular canal is shown at *sc.c.* (*From Quain's Anatomy, Longmans, Green & Co.*)

at right angles to one another so that they permit a resolution of linear accelerative forces in two dimensions.

414. The Mechanisms of the Sense-Organs. — The general manner of operation of these sensory mechanisms can be understood quite readily. In the case of the maculae, we may suppose the hairs to be deflected in directions which are determined by the orientations of the receptor surfaces with respect to the gravitational field. This deflection is referable to the fact that the otoliths have a much higher specific gravity than has the endolymph, so that they tend to sag, dragging the mucus and hairs with them. When a linear acceleration is added to the gravitational force, the effect will naturally conform to the resultant of the two factors. The exact distribution and intensity of the pull, over the receptive fields of the four maculae, should suffice to represent the exact nature of the given orientation.

The semicircular canals are obviously well adapted for the analysis and recording of *rotatory* accelerations of the head. If the head begins to turn about an axis which is perpendicular to the plane of any one of these canals, there will be a tendency for the endolymph within the canal to lag behind, since it can be set into motion only by virtue of its friction with the canal walls. Consequently, in the beginning, there must be a relative motion between the endolymph and the cristae. This should deflect the hairs and their attached mucous masses in a direction which is characteristic of that of the given acceleration. If the rotation is brought to a constant velocity, the endolymph will soon catch up with the motion of the canal walls, so that the hairs will then assume their normal positions, and excitation will cease. If, then, the head is quickly brought to rest, the endolymph will tend to remain in motion, and there will be a deflection of the hairs in the opposite direction. The cristae of the other canals will not be excited, under these conditions, since there will no components of rotation in their particular planes of space.

However, if the plane of the rotation does not coincide exactly with that of any one of the three canals, there will be a resolution of accelerative vectors among the canals, and the various cristae will be excited in a quantitative ratio which will be characteristic of the actual plane of the rotatory forces. Consequently, the apparatus seems adequate to record, not only the direction, but the exact plane of the action. Strictly speaking, the mechanism of the semicircular canals does not respond to acceleration, as a mathematical entity, since it continues to be excited after the acceleration is over, in the interval during which the endolymph is catching up with the canal walls. Under such conditions, accelerations in an opposed sense would only serve to remove the state of excitation. However, all of these peculiarities agree with the psychophysiological facts.

It has been argued that the extreme fineness of bore of the canals precludes the notion that there can be an appreciable lag of the liquid in relation to rotatory accelerations of the head. However, this would seem to be a purely qualitative argument without actual quantitative foundations; no matter how small the bore may be, there must be some lag so long as the endolympth is not a solid. Since we have no knowledge regarding the amount of relative displacement which is needed to excite the cristae, the objection seems to be gratuitous. The notion that we can substitute a " pressure " for an actual relative flow of liquid must be rejected, since there could be no pressure without some displacement in a system of this sort. The temporal relations of the vertigo experience indicate that the relative flow of the endolymph is considerable and that the establishment of a stationary condition requires a rather long time.

415. Psychophysiological Correlations of Inner Ear Response. — We must suppose that what we have called the *kinaesthetic vertical* is determined by the continuous excitation of the macular receptive field, which involves four groups of receptors, in the utriculus and sacculus of the right and left ears. The direction of the vertical with respect to the system of experience as a whole must depend upon the exact pattern of the excitation on this general receptive area. This pattern changes specifically, as we have seen, as a function of the inclination of the head with respect to the gravitational-accelerative field.

The *vertigo experience* is determined, similarly, by the displacement of the hairs of the cristae from their normal equilibrium positions. The experience is entirely absent when the hairs are undisplaced, so that the excitation must be regarded as phasic, rather than tonic as in the case of the macular sense. The intensity of the vertigo rests upon the degree of the displacement; its plane, upon the ratio of the excitation between the three pairs of canals; and its direction, upon the direction of the displacement itself with respect to the normal position.

These views are confirmed by experiments in which the inner ear is excited by electrical and thermal stimuli. Under such conditions, there are apparent movements of the head and body in experiential space, accompanied by nystagmic displacements of the eyes. We must, of course, assume that the excitation of these sense-organs sets off specific ocular reflexes, responsible for the peculiar visual effects which accompany vertigo. The pioneer experiments of Flourens,[653] on the behavior of animals from which the semicircular canals had been removed by operation, also confirm the theory in detail.

416. Neural Relations of Absolute Kinaesthesis.— No general difficulties appear in regard to the neurological relationships of experience in this department of sensation. Apparently, we are concerned merely with an *intensity* transmission, which can readily be carried in terms of nerve pulse frequency. The receptors presumably operate in the same manner as those for touch or motor proprioception, the impulse frequency depending upon the degree of distortion or stretching of the cells. Possibly, the excitation may be due directly to a mechanically induced increase in the permeability of the cell membrane, at certain points where the stretching action is at a maximum. The directional features of the experiences evidently rest upon the exact pattern of distribution of the nerve impulses over the total afferent nerve fibre system, within the given sensory department.

The vestibular branch of the eighth nerve has important connections with the cerebellum as well as with the cerebrum. Sherrington,[654] in fact, characterizes the cerebellum as the "ganglion of the proprioceptors," and it has been shown that, in animals, extirpation of the cerebellum produces an effect upon behavior which is very similar to that resulting from the removal of the proprioceptors of the inner ear. The exact form in which the nerve currents from these organs reach the cerebral cortex must be determined, to a very considerable extent, by processes in the subcortical centers involved in controlling the highly complex reflex adjustments which rest upon their excitation. Such adjustments concern not only eye-movements, but the equilibration of the entire musculoskeletal system. It seems to be true that the direct representation of this elaborate mechanism, within consciousnenss, is relatively quite meagre. However, the consequences of the reflex adjustments are, of course, reflected in modifications of experience through many different channels of sensation. It is difficult to agree with Lussana's [655] suggestion that the absolute kinaesthetic experiences may be directly correlated with cerebellar activity.

Section 72

RELATIVE KINAESTHETIC SENSATION

417. Kinds of Relative Kinaesthesis. — We have seen in our chapters on perception (Volume I, see also Note F) that experience contains definite features which are correlated with the positions, tensions, and movements of the musculoskeletal system. The introspective analysis of these kinaesthetic experiences is difficult, but, according to Titchener,[656] it is possible under proper conditions to distinguish between three qualitatively different species, which he supposes to be determined by receptors in the muscles, tendons, and joints, respectively. We have already designated these three forms of experience, subjectively, as exertive, tensive, and attitudinal. They are all similar, in general, to cutaneous touch, but have special qualitative colorings which permit them to be identified introspectively. Titchener characterizes the exertive experiences as " dull, dead and diffuse," the tensive as " bright and thrilling," and the attitudinal as " massive " and more closely similar to cutaneous touch than the other two. All three of these kinds of experience tend to be localized within the volume of the experiential body, although frequently reaching its surface and fusing there with the touch and thermal qualities. Sometimes, however, they are " projected " into external space and are regarded as properties of tactual *things*.

418. Stimuli to the Musculoskeletal Proprioceptors. — We cannot doubt that each of these species of kinaesthetic experience is correlated with the activity of special kinds of receptors and particular afferent nerve channels. These receptors must be sensitive to characteristic forms of energy or force which arise within the musculoskeletal system. We are well acquainted with the existence and structure of receptive organs in the system in question, and have accumulated considerable knowledge concerning their physiological action. However, there is a serious lack of experimental evidence bearing upon the specific psychophysiological correlations of these receptors. Hence we are compelled to argue largely on the basis of general principles and probabilities.

If we accept the Titchenerian three-fold division, and consider the mechanics of the musculoskeletal system (see Fig. 95), it would appear that the corresponding stimuli should be as follows. For the *exertive* experiences: contraction or elongation of the muscles or the individual fibres of which they are composed. This amounts to a deformation of the muscular tissue, and hence is analogous to the stimulus for cutaneous touch. It is conceivable that the deformation may require an active or innervated contraction of the muscle, but it is more likely that either active or passive deformation will be effective, although possibly with differences in degree. For the *tensive* experiences: tension in the tendons, or the stretching distortion of the tissues which results therefrom. Tension can be expressed in terms of force per unit of cross-sectional area. The stretching or strain which follows in consequence of such stress must involve both elongation of the tendon and a corresponding reduction of its cross-section. The stimulus is thus mechanically similar to that in the case of muscle, but it presumably involves more force and less change in form, and the forces are externally impressed rather than internally generated. For the *attitudinal* experiences: pressure gradients or tensions in the tissues which are associated with the joints or articular surfaces. These include the articular ligaments, the synovial capsules, the periosteum, and the ends of the bones themselves. Here, again, the stimulus has the same general mechanical nature as in the case of the muscles and tendons, but is probably more complex in its details, depending upon the exact articu-

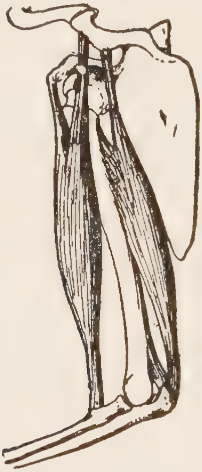


FIG. 95. TYPICAL MUSCULOSKELETAL APPARATUS.

This drawing, by Stiles, shows the bones of the human arm and shoulder, together with the biceps and triceps muscles and the tendons which connect them to the skeletal parts. Proprioceptors are found in the muscles, the tendons and the membranes of the joints. (*From Stiles: Human Physiology; W. B. Sanders Co.*)

lar tissue which is primarily concerned. We are tempted to think of the joint as providing a receptive surface, similar to a portion of the skin, upon which a pressure pattern can be impressed, this pattern being a reliable function of the relative positions of the skeletal components which are involved. It is not necessary, for this purpose, that the entire area of the joint should be sensitive. An envelope of sensitive tissue forming a border about the articular interface would be entirely adequate.

419. Attitudinal Experience as a Function of Stimulus Factors. — *Evidence for Articular Sensibility.* — As already indicated, we are very poorly supplied with information concerning the sensory relationships of the relative kinaesthetic experiences, regarded as the correlates of individual receptive systems. In our discussion of stimuli, above, we have assumed that the attitudinal experiences are correlated with the distribution of forces in the articular tissues. This view is strongly favored by Titchener,[657] Luciani,[658] Goldscheider,[659] and Lewinski,[660] but is vigorously opposed by Pillsbury,[661] Winter,[662] and others. For reasons which we have already suggested, the attribution of the attitudinal sense to the articular surfaces commends itself logically. If this is not the actual foundation of the sense in question, then evolution "missed a good bet," and utilized a far more difficult means for recording the bodily postures and movements. Indeed, we might reasonably argue that definite and reliable specification of posture in terms of muscular deformations or tendinous stresses is impossible. Of course, it is true that all normally attainable postures correspond with definite patterns of muscular innervation or contraction, but the reconstruction of these patterns in the brain centers on the basis of intensity ratios between the nerve currents proprioceptively derived from the various motor antagonists would seem to be a difficult task.

We may now regard it as definitely established that the efferent innervations, themselves, are innocent of all part in the determination of the kinaesthetic experiences. Here, again, it might seem that evolution "missed a good bet."

But the function of kinaesthetic sensation seems to be to represent the postures or movements which actually occur, rather than those which are merely intended. The latter receive representation in the form of kinaesthetic imagery. Moreover, it appears to be a general principle that experience is based upon afferent and not upon efferent aspects of the cortical process. Many cases have been reported in which a patient has lost all conscious representation of his own posture and movement, but is still able to innervate his muscles more or less adequately.[663] Lashley[664] has described one case in which the accuracy of such movement was as great as under normal conditions, although the individual was quite insensitive to his actual motor status.

Although, under ordinary conditions, touch and kinaesthesis are closely associated, we can readily conceive that an adequate representation of the postures and movements of the parts of the body might be given in terms of touch alone. However, in pathological cases where cutaneous sensibility is unaffected while that of the motor tissues is obliterated, the patient has no conscious representation of his bodily posture when blindfolded.[665] Strümpell[666] has reported a case in which the muscular and tendinous proprioceptive systems were unaffected, but the articular system was anaesthetic. The individual had no consciousness of his postures or movements. Duchenne,[667] on the other hand, describes a case in which muscular and tactual sensibility were lost, but joint sensibility was retained. Here, the posture and movement experiences still persisted.

Although criticisms of these observations may be possible, they seem more convincing than the evidence on the other side (Pillsbury) which merely shows that certain previously alleged proof of the importance of the articular sense is not conclusive. Goldscheider[668] found that faradic anaesthetization of the joints seriously interferes with movement perception, while Winter[669] reports that similar treatment of the muscles and tendons has a much more serious effect. Pillsbury,[670] however, produced an equally great disturbance by faradization of wholly irrelevant portions of the body, so that tests of this sort seem to be quite inconclusive.

Our views concerning the exact psychophysics of the articular sense must be largely conjectural. It seems reasonable to treat the attitudinal experiences as constituting a spatial mosaic which has a part-to-part correspondence with the total articular receptive field. The intensity of the experience is independently variable at each experiential point, and such intensity values are determined by local pressure factors in the corresponding portion of the "sensifacient" system. The laws of such determination would presumably be similar to those which hold for the sense of touch. The pattern of distribution of the pressure variables over the receptive field will thus govern the correlated kinaesthetic configuration, or "conscious attitude," in experience. Observations made by Lewinski upon his ataxic patient confirm this general view. When standing erect, this patient felt his leg to be bent at the knee, but when reclining this illusion disappeared. Presumably, the nerves supplying one side of the joint surface were more seriously impaired than those of the other side, but when pressure was removed from the system as a whole the asymmetry of the excitations was relieved.

Thresholds. — It is natural that the absolute and relative thresholds for intensity of stimulation of the articular sense should not have been determined. Extant quantitative data seem to be limited to the conditions for just-noticeable movement. Goldscheider[671] found that angular displacements as small as 0.22–0.72 degrees could be detected at some joints. The angular threshold decreases with increase in speed and the speed must exceed 0.25–1.4 degrees per second (varying with the identity of the joint) in order to arouse a movement impression, under any conditions. According to Goldscheider, the threshold is practically independent of the starting position of the moving part, although Winter finds it to vary in this regard. The sensibility to active movement is only slightly greater than that to passive. (It is possible to execute voluntary movements which are too slight to be sensed.) The increase which is actually observed can probably be attributed to the augmented pressure at the articular interface. It can be shown experimentally that such an increase of pressure favors the appreciation of movement, while a decrease — produced by pulling on the limb — is unfavorable. Most of these observations seem to corroborate the articular theory of the attitudinal experiences.

On account of the comparative permanence of these experiences, we must suppose that the sense is relatively nonadaptive. However, prolonged maintenance of a fixed posture, as in sleep, frequently results in the complete lapse of the attitudinal impression, which is restored by a movement, changing the pattern of stimulation of the receptive field.

420. Tensive Experience as a Function of Stimulus Factors. — Tensive experiences accompany the lifting or supporting of weights, the overcoming of frictional or elastic resistance, etc. We have already considered some of the relations which hold between these experiences and the objective dynamical factors in the situation. Absolute thresholds can be determined in terms of such objective conditions, and Weber's law can be shown to hold (at least approximately), with reference to the forces which are applied or exerted, externally. Now, it seems most reasonable to suppose that these tensive experiences are correlated with the tensions in the tendons, or closely adjacent portions of the muscle, since these are the points at which the operative mechanical forces are most completely and reliably represented. It is entirely conceivable, however, that the function should be shared by the tendons and the muscle as a whole. Allers and Borak[672] have studied the sensibility to lifted weights in individuals who have been operated upon in such a manner as to eliminate the joints and more distant tendinous attachments. They find that the sensitivity to difference in weight, and to movement, is as good as in the normal person.

In order to reduce the study of these relationships to a sensory basis, it will be necessary to identify and to compute the exact forces which act upon the specifically sensitive tissues. If these are the tendons and the muscle facia, we must apply the law of the lever, and compute the forces in question from the given lever-arm and weights. We have already noted that the absolute threshold is a function of the exact point along the length of a limb at which the weight is supported, as well as of the identity of the joint which forms the operative fulcrum. Using a special method to minimize the influence of touch, von Frey found that the same weight placed at the wrist felt heavier than at the elbow, when the muscles of the shoulder were concerned.[673] The weight also feels heavier when rapidly accelerated, owing to its mass effect. Von Frey finds the relative differential threshold, under the conditions of his tests, to be nearly as fine as that for visual brightness (1/100). Practically no careful analyses of the tensive sense from the strictly sensory point of view are available, although the work of von Frey, just quoted, indicates the proper line of attack.

Adaptation. — Allers and Saito[674] find that the sensibility to differences in weight is increased by a single vigorous muscular effort, but is decreased by continued exertion. Borak[675] notes that the sensibility is better when the lighter of two weights is lifted first than when the opposite procedure is employed. This may perhaps be attributed to a difference between the fatigue effects in the two cases. The following striking experiment, which may readily be performed by anyone without special apparatus, can also be attributed to adaptation of the tensive sense. Stand erect, with the arms straight at the sides, facing along the length of a wall. Press the back of (say) the right hand against the wall for a minute or two with strong exertion, using the muscles of the whole arm. Then step away from the wall. It will be found that if the arm is kept straight, it will rise from the side and come to equilibrium in an elevated position, the exact angle of which will be determined by the degree and duration of the previous exertion. If a voluntary effort is made to bring the arm down to the side, a tensive experience arises which increases in intensity with the degree of departure from the equilibrium position. If the arm is allowed to stay in its elevated position, it will fall very gradually until it finally hangs vertically.

These phenomena can be explained on the assumption that the balance of innervations between the flexors and the extensors of the arm is determined by a corresponding equilibrium between the nerve currents from the proprioceptors of these muscles. The protracted pressure of the arm against the wall fatigues the receptors in the extensor system and allows those in the flexor system to recovery unduly. Upon removal of the external restraint, the system automatically adjusts itself to a neurological balance, which demands increased tension in the tendons of the extensors. Voluntary innervation to overcome this condition leads to an increase in the proprioceptive excitation for the flexors above that which is normal for the given position of the arm, and hence gives rise to tensive experience.

421. Exertive Experience as a Function of the Stimulus. — Our knowledge of the stimulus conditions for experience of the type classed by Titchener as "muscular sensation" is almost nil. This quality is probably identical with that aroused in connection with the so-called "deep sensibility" noted by Head and Rivers (*cf.* page 296, above), and other investigators, under conditions of cutaneous anaesthesia. Heavy pressures are sensed as dull, diffuse contacts, under these circumstances. Intense muscular work gives rise to similar feelings. They can also be evoked by bringing about the contraction of muscles with electrical stimuli. Feelings of this sort are definitely to be distinguished from muscular fatigue and pain, which we shall consider below.

422. Musculoskeletal Proprioceptive Processes and Their Correlations. — The tissues of the muscles, tendons, and joints contain a wealth of receptive end-organs, and the mechanical stimulation of these tissues has been found to yield definite reflex effects. One of the most recent of the latter to be studied is the so-called *stretch reflex,*[676] which consists in an active contraction of the muscle in response to passive stretching. It has been shown that this result can be obtained through conductive circuits confined to the muscle, itself, without the assistance of external nerve centers. The importance of the afferent nerve-system of muscles is shown, however, by the high ratio of sensory to motor fibres in muscular nerve trunks; ordinarily, there are half as many of the former as of the latter, and sometimes they exist in equal numbers.[677] The receptors which are found in the muscles and tendons include Pacinian corpuscles of several types, basket and tendril terminations, Golgi-organs, and muscle spindles. The latter are particularly characteristic of the muscles and the Golgi-organs of the tendons.

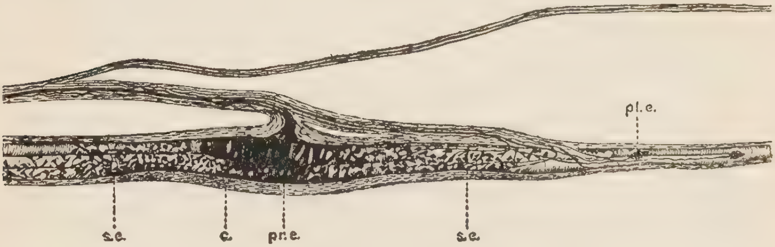


Fig. 96. A Muscle Spindle.

This is a representation, by Ruffini, of a muscle spindle from the cat. *pr.e.* is a primary nerve-fibre ending, *s.e.* a secondary ending, and *pl.e.* a plate ending. They are all probably sensory in function. *c* is the capsule of the spindle. (*From Starling: Principles of Human Physiology, Churchill.*)

The typical muscle spindle consists of a number of active muscle fibres, around which a nerve termination is closely coiled. (See Fig. 96.) The contraction of the fibres must stretch or compress the coil, and presumably stimulates it mechanically. The studies of Sherrington[678] demonstrate the sensory character of these spindles quite conclusively. He regards them as muscle "length-recorders," but we have no definite proof that they are concerned in the evocation of kinaesthesis. It seems quite certain, on the other hand, that they are the specific receptors for the stretch reflex. The

Golgi-organs (Fig. 97) and Pacinian bodies which are found in the tendons are well adapted in form and position to be stimulated by the internal pressures which are developed in these tissues. Sherrington designates these receptors as tension-recorders. The cartilages of the articular surface are free from nerve-ends, but the latter are abundant in the synovial capsules, the articular ligaments, the periosteum, and even the ends of the bones. The commonest form in this region is a modified Pacinian corpuscle.

Tentatively, we may assume that the muscle spindles are the receptors for the *exertive* sense. Although it seems highly probable that they are also the afferent organs for the stretch reflex, the experiments of Forbes,[679] Adrian,[680] and others have shown that they contribute impulses to nerve trunks leaving the muscle. It is likely that these impulses do not reach the cerebral cortex in appreciable measure until the excitation of the spindles becomes quite powerful and extensive. This would account for the seemingly low sensitivity and dullness of the exertive system.

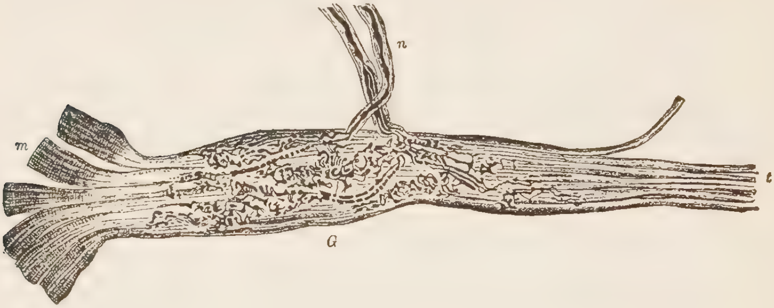


FIG. 97. GOLGI-ORGAN FROM HUMAN TENDON.

This figure represents a preparation, by Ciaccio, from the human tendo achillis. At *m*, the terminations of muscle fibres are seen; at *t*, tendon bundles; at *G*, an organ of Golgi; and at *n*, afferent nerve fibre attached to the latter. (*From Quain's Anatomy; Longmans, Green & Co.*)

The *tensive* qualities may be assigned provisionally to the Golgi-organs of the tendons and related tissues, although there is no reason for ruling out the Pacinian corpuscles of the tendons and muscle sheaths. The Golgi-organs are particularly numerous in the regions where the tendons connect with the muscular tissue proper. Their relatively great length, along the axis of the tendon, suggests a special sensitivity to slight stretching or longitudinal tension. It has been shown that these receptors are not concerned in the stretch reflex, and that they are particularly well developed in the higher mammals.

The attitudinal experiences will naturally be attributed to the modified Pacinian corpuscles of the articular tissues. Our knowledge of the receptors of the joints appears to be in a particularly unsatisfactory condition. In view of the seemingly great psychophysiological importance of these receptors, a more detailed investigation of their exact nature and distribution is greatly to be desired.

423. Neural Correlations of the Relative Kinaesthetic Experiences. — Although our knowledge of the psychophysiology of the musculoskeletal proprioceptive system is in such an unsatisfactory state, we may nevertheless suppose that its conductional principles are generally similar to those for other sensory departments. Intensity, on the subjective side, is determined by the number of quantal nerve impulses delivered per second along a group of coöperating fibres. The quality of the experience is determined by the anatomical identity of the fibres in question, and the experiential space pattern is a function of the distribution of impulse density over the entire system of fibre groups.

It is interesting that the first demonstration of the nerve current due to stimulation of a *single* receptor should have been made with respect to muscular proprioceptors. Adrian and Zotterman [681] have recently succeeded in electrically recording the nerve current which is aroused by the passive stretching of a single muscle-spindle. They found that there is a regular series of impulses, increasing in frequency with amount of stretch, but declining gradually with time for any given constant elongation of the muscle. Forbes, Campbell, and Williams [682] have shown that active contraction of a muscle also yields proprioceptive impulses which can be electrically recorded. Usually there are two groups of such pulses, one due to the contraction and another referable to the subsequent process of muscular relaxation.

Section 73

INTERNAL SENSATION

424. The organic conditions which determine specific experiences localized within the body have been discussed, under the heading of perception, in Volume I. For the convenience of the reader, this discussion has been reproduced in Note G. The experiences in question include hunger, thirst, organic pain, sexual feeling, and the like. In that discussion, we have considered these experiences as being perceptually related to the particular organic conditions which are involved. A sensory analysis of these same systems would necessitate a more intimate knowledge of the receptor processes and of the manner in which the given organic states excite them. We should also have to consider the nature of afferent nerve-currents in each case. Unfortunately, as we have already noted, there is practically no available information concerning these questions. Thus, for example, regarding hunger, we can only say that it rests upon a certain chemical state of the stomach walls, combined with muscular contractions thereof, but we cannot identify the receptors or give particulars concerning their exact manner of stimulation.

In general, we may suppose that each of the internal senses involves a specific afferent nerve path, and that transmission along such paths follows the law of simple impulse frequency. The intensity of the corresponding experience will increase in proportion to the frequency. The quality of the experience, on the other hand, will be determined by the identity of the given afferent path, in conjunction with its attached cortical mechanisms. The spatial and temporal characteristics will depend upon the distribution of the excitations over the given field of conductors, either in space or in time.

Chapter XIX

Generalizations Concerning Sensation

In the present Part of this book, we have treated the problems of sensation as having to do with the relations between experience and various features of the afferent arc process. We have conceived this process as beginning with the stimulus, and as including the receptor activity, and the afferent nerve excitation and conduction. We have traced the experimentally demonstrated and probable relationships of experience to these various factors, for the several distinguishable departments of afferent conduction. Each of these departments has its own special characteristics, and it is somewhat difficult to lay down any very general principles of sensory physiology.[683] However, a few comments can be made along this line.

425. **Foundations of Intensity and Quality.** — Probably the safest generalization which can be made is that the intensity factors in experience, as well as in the stimulus, are correlated with the frequency of the impulses in the corresponding nerve currents. It appears likely that the experiential *intensity* is at least approximately proportional to the neural frequency, other things equal. These "other things" include the activities of adjacent fibres, which may combine into a unified process. Where such combination occurs, the intensity is presumably determined by the total impulse frequency in the composite conducting unit. We may feel quite safe in placing the locus of the Fechnerian logarithmic relationship between the stimulus and the nerve conduction process, in practically all cases of intensity transmission.

The *qualitative* aspects of experience appear to be determined in a number of different ways, with respect to afferent arc processes. In the majority of cases, the quality seems to depend upon the mere anatomical identity of the conducting nerve paths. However, in the case of audition, we have supposed that the impulse frequency is also involved. The exact manner of spacing of the impulses, whether regular or irregular, is assumed to enter into the determination of the auditory quality. Similar relationships have been suggested for olfactory and visual response. In general, we can hardly believe that mere anatomical identity can actually suffice to yield qualitative differences in consciousness. We shall be compelled to postulate special cortical substances at the terminations of the respective afferent paths.

426. Spatial and Temporal Determinants. — We have not confined our study of sensation exclusively to intensive and qualitative differences, but have dealt also with spatial and temporal patterns, insofar as these are determined by afferent-arc factors. In general, it appears that, in certain receptive fields, the pattern of the stimulus can determine that of the entire afferent-arc process. Within the conducting nerve cables, the pattern must involve a particular spatial distribution of excitation among the many component fibres. Temporal patterns must be correlated with special modes of change in the afferent conduction, from one time to another. The recent studies of Adrian [684] combine with other evidence to make it quite certain that processes of adaptation are receptoral in their origin. Contrast effects, however, are probably primarily neural and largely cortical in source.

The study of sensation, like that of perception, is very far from providing us with the final resolution of any of these questions. Both of these lines of inquiry are merely introductory to the study of cerebration, which will concern us in Volume III, and which should yield a complete understanding of the psychophysiological nexus, when adequate data are at hand.

Notes

These Notes are reproductions of certain paragraphs in Volume I, which deal with matters presupposed in the discussions of the present volume. They are appended here, with references in the text, for the convenience of the reader who may not have the first volume at hand. The index numbers in these Notes indicate works listed at the end of Volume I.

NOTE A. THE INTROSPECTIVE PSYCHOLOGY OF COLOR.

128. *The Definition of Color.* — The word color has numerous more or less discrepant meanings in scientific, as well as common-sense, discussions.[214] Ordinarily, when used in the affirmative mood, it includes those visual qualities which exhibit hue and saturation — that is, which are to some extent reddish, yellowish, greenish or bluish — and excludes black, white and intermediate grays. In the interrogative mood, however, color frequently becomes sufficiently comprehensive to include black, white and the grays, so that it becomes the universal name for elementary visual qualities of the species which we wish to consider. It is in this comprehensive sense that we shall employ the word.

Physicists frequently use the term, color, as a synonym for wave-length,[215] or wave-length composition, when speaking of radiant energy. This usage, however, is at the present time coming under a ban, since physicists are recognizing that color is wholly a psychological or introspective phenomenon, having no place in the world of energy and atoms. Since, in this way, we regard color as wholly psychical in its nature, we shall find it unnecessary to speak of "color sensations" or of "sensations of color." The problem of color sensation is concerned with the determinative relationships which hold between color and various characteristics of the stimulus, sense-organ, and receptor stages of visual response. We might, perhaps, assert that color is a *sensation or perception of radiant energy*, but this would add nothing to our exposition of the facts.

129. *The Classification of Colors.* — Introspection shows that, although a very large number of qualitatively different colors are given in visual consciousness, this number is nevertheless definitely restricted, so that it is readily possible to form *a catalogue of all possible colors.* Upon comparing such colors amongst themselves, it becomes evident that they exhibit resemblances and differences which invite classification and the formation of a system. A preliminary study of these relationships leads us to divide colors into two general classes, which we may call the *achromatic* and the *chromatic*, respect-

ively. The former consists of black and white, with a long series of intermediate grays. The latter consists of all colors which we can describe as reddish, yellowish, greenish or bluish. It may seem a contradiction in terms to speak of "an achromatic color" and a redundancy to refer to "a chromatic color," but it will be seen that this is not the case if color is defined in the broad way above indicated and if, on the other hand, we employ the term, *chroma*, as a synonym of the common affirmative use of the word, color, in the restricted sense.

130. *The Achromatic Series.* — If we contemplate the achromatic colors, it becomes evident that they can be arranged into a quantitative series, in accordance with our general criterion for the production of a psychological system. If we dispose all of these colors, or grays, as we may call them (including black and white), so that the sum of all of the differences between neighboring members of the arrangement is a minimum, we arrive at a linear, or one-dimensional, system. The limiting members of this system are black and white, the intermediate ones being various grays, ranging from dark grays near black to light grays near white. The natural reference point of this linear system is the gray which is midway between black and white, and which is called the mid- or *median gray*. If this scheme of achromatic colors includes all possibly discriminable grays, and no duplicates, each member will be just noticeably different from its neighbors. Since this is by definition a unit difference, it becomes possible to specify any gray numerically in terms of its position in the series, with respect to some arbitrarily determined reference member, such as the mid-gray. According to Külpe,[216] the number of members in such a series is 810, while König[217] puts the number at 660. Referred to the mid-gray, other achromatic colors would be measured by positive and negative numbers, the former finding a maximum in white and the latter a maximum in black. Although, actually, it is difficult to identify the ideal black and the ideal white, it seems best to specify the position of any gray in the series by reference to black as number No. 0, so that all of the numbers are positive, white having the highest position. This scheme enables us to define a concept of *brilliance*, which is a color attribute determined by the scale of grays and corresponding to our general notion of apparent "brightness." In practice we shall be obliged to identify black with the darkest gray which we can find, while white will consist of the lightest of all realizable grays.

131. *The System of Chromatic Colors.* — The peculiar nature of the chromatic colors, as contrasted with the achromatic ones, seems to be evidenced by our sharp distinction in common discussion between "colored" and "colorless" objects, the former possessing the attribute which we here call *chroma*. However, a study of a representative collection of chromatic colors shows at once that they also possess the characteristic attribute defined by the achromatic system, namely brilliance. Hence we may proceed at once to consider the properties of a group of chromatic colors which are all possessed of the same or *equal brilliance*. If we arrange all possible *chromas* of this sort into a system, such that the sum of the differences between all neighboring members is reduced to a minimum, we find that they form a two-dimensional manifold, or a surface. (See Fig. 7.) We discover, however, that there is a single point in this surface which is naturally reserved, on account of the similarities and differences of adjoining colors, for the unique achromatic color which possesses the brilliance value common to all of the chromas in the arrangement.

This unique achromatic color, or gray, furnishes a natural reference point for the chromatic attributes in general.

Since the dimensions of the chromatic system, above established, are two in number — corresponding to the surface or plane character of the system — there must be *two independently variable* chromatic attributes. These attributes, as ordinarily defined, consist of hue and saturation. *Saturation* is measured radially in the chromatic plane, with respect to the single gray component as a reference point. In other words, as expressed for any chroma in terms of number of just noticeable difference steps from the gray, it is a measure of the degree of difference of the chroma in question from an achromatic color of the same brilliance. However, it is evident, from the fact that there are a large number of radial systems in the plane, that there must be a second dimension which is always perpendicular to any given radius, or which, in other words, has a tangential or cyclic direction. This second chromatic dimension or attribute is of course that of *hue*. Hue, thus defined, will naturally be measured in terms of the number of just noticeable differences from some standard point or radius, along a circle having the gray point as a center. Such a circle will be defined as a series of colors, varying in hue, but having equal saturations as well as brilliances. This means that they are separated by equal numbers of liminal steps from black and also from the gray of the same brilliance.

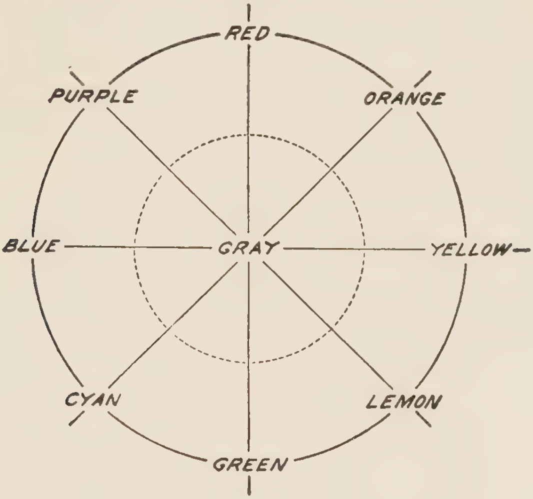


FIG. 7. COLOR CIRCLE, SHOWING THE RELATIONSHIPS OF COLORS OF A SINGLE BRILLIANCE VALUE.

The four psychologically primary hues are represented on the periphery of the circle, together with four intermediates. The gray of the same brilliance lies at the center of the circle. Saturation is measured outwardly along any radius, while hue follows the circumferential dimension.

132. *The Psychological Color Solid.* — When we consider chromatic surfaces or planes of different brilliances, it becomes evident that these must be arranged, so to speak, into a pile, so as to form a solid figure, the axis of this figure consisting of the entire system of *achromatic* colors. In this way, we inevitably arrive at a construction which includes all possible colors, whether chromatic or achromatic, and the total system must possess three dimensions, corresponding respectively to the three attributes known as brilliance, hue and saturation. The simplest external form to assign to this system is that of a cylinder, the axis of which comprises the grays, while various radial planes contain individual hues, having saturations that vary with the distance of any point or line in such a plane from a perpendicular to the axis. (See Fig. 8.)

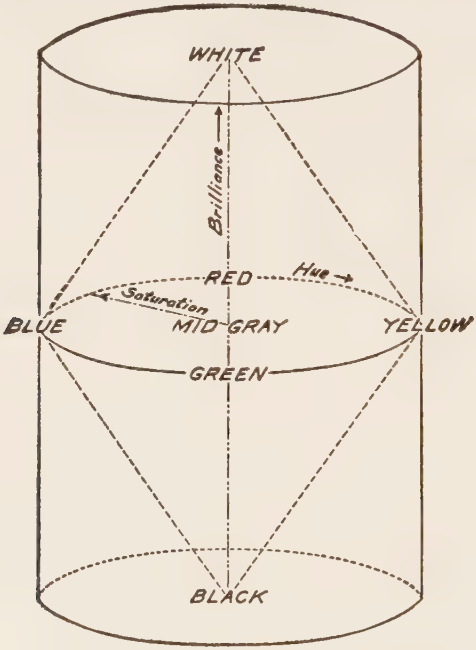


FIG. 8. THE PSYCHOLOGICAL COLOR SOLID.

The essential purpose of this diagram is to reveal the three-dimensions of psychological color space. For this purpose, the color solid is represented as a cylinder, although the alternative form of a double cone (indicated by the dotted lines) may perhaps be preferable. See the text for complete explanation.

However, it should be noted at once that the question as to whether the psychological color solid is a cylinder, or some other figure, is one which rests upon psychophysiological evidence and has nothing to do with the definition of the color system in itself. Indeed, the latter consists simply in a kind of conceptual space, having no definite boundaries, although possessing an arbitrarily established reference system, or set of axes. This space of the color system does not necessarily have the same mathematical properties as does geometrical or physical space. In other words, it may not be Euclidean. As an illustration of this possibility, it may be noted that there is no particular reason why the ratio between the saturation of a cycle of equally saturated chromas and the number of just noticeable hue steps in such a cycle should be equal to 2π, the corresponding ratio of the radius of a geometrical circle to its circumference. The conceptual color space may perhaps be compared to some of the non-Euclidean spaces of modern physical theory.

It is evident that the identity of any color can be specified completely in terms of its position in the color space. This position is represented, in fact, by the measures of the three color-attributes for the individual color in question. These measures correspond to the three coördinates, X, Y and Z, of a point in three-dimensional physical space, as the latter is treated in analytical geometry. It is very doubtful whether, ultimately, the three attributes of color can be given any other meaning than that which is embodied in the structure of the color space. It is wholly evident that no color possesses in itself a triplex constitution, each color being absolutely simple and indivisible. The complexity which compels us to describe a color in terms of three variables lies entirely in the external relations of similarity and difference between the given color and other similar qualities. Any color by itself is thus no more complex in constitution than is any geometrical point, although both have three coördinates.

133. *The Psychological Primaries.*—It is an interesting question as to why we have placed the reference axes of our psychological color space in the positions which they ordinarily occupy. Theoretically it would be possible to rotate these axes, or otherwise displace them from their present position, without interfering with the specification of color qualities in terms of three attributes. Under such conditions each dimension would be some peculiar resultant of the three attributes which we now call hue, saturation and brilliance.[218] It seems quite probable that our positioning of the axis system has been dictated by common psychophysical considerations, such as that the *brilliance* of a color is especially conditioned upon variations in the *intensity* of the stimulus. However, there is another possible view, which is that certain points in the color space possess unique relationships of similarity or difference with respect to their neighbors, so that they can be singled out, by a purely introspective test, as natural reference points.

A demonstration of the possibility of such a psychological origin for reference points in the color system is found in the almost universal admission that red, yellow, green and blue are *unique hues*, in terms of which all other hues can be described, but which are themselves indescribable in terms of other hues. Black and white also seem to possess this same sort of uniqueness. Any gray can be described as a blackish white, while orange is specified quite intelligibly as a reddish yellow, but no one would know what was meant by a " reddish green " or a " yellowish blue," unless he had studied the psychophysiological relationships of colors and stimuli. There has been a great deal of debate concerning the validity[219] of these so-called psychological primaries, black, white, yellow, red, green and blue, but very little has been accomplished by way of elucidating their significance. To the present writer, it seems that a wholly introspective justification of their selection can be established if we admit the possibility of comparing and discriminating, not only the colors themselves, but also *differences* between separate pairs of colors. Thinking in this way, we can recognize that the difference between red and orange is the same, qualitatively, as that between orange and yellow, while the latter difference is itself different from the difference between yellow and yellow-green. Thus, the psychological primaries would be defined as colors which lie at points of *sudden transition in the mode of variation* from one point of the color space to another. These ideas involve us in a sort of calculus of qualitative differentials or derivatives, analogous to the quantitative concepts with which mathematicians are already familiar.

134. *Boundaries of the Color Solid.* — As above indicated, we can only ascertain the boundaries of the psychological color solid by experimental studies, directed towards determining what is the widest variety of colors that can actually exist. A consideration of such experiments forms a natural part of the psychophysiological portion of our discussion, but a few words are required in anticipation in order to set aside some extant misconceptions. In the first place, it should be noted that the representation of the color solid as a double pyramid or other *four-sided figure*, on the basis of the uniqueness attached to the psychologically primary hues, is incorrect both logically and experimentally. Such a representation, as given by Titchener [220] and others, implies a necessary relationship between psychological primacy and saturation, whereas in fact no such relationship can exist, because the concepts of hue and saturation are so defined as to be independent of each other. Psychological primacy can be represented in the color solid only by means of lines or points laid down within it in certain positions. It has nothing to do with the boundaries of the solid. Another important misconception identifies the equator of the figure with the spectral colors, and regards the latter as being of equal saturation. As a matter of fact, it is easy to produce colors which are much more saturated than the normal spectral colors, and the latter are very far from being of equal saturation, although the *purity* of the physical stimuli is perfect. But the most important point in the present discussion lies in the fact that the spectral colors must depend, for their location within the color space, upon detailed psychophysiological measurements.

135. *Other Color Attributes.* — Hue, saturation and brilliance do not exhaust all possible attributes of colors, since it is possible for them to vary in dimensions distinct from any of these three. Any psychical element is said by Titchener [221] to possess the attributes of intensity and duration, and possibly extensity. It is possible that we should not identify intensity with brilliance, in the case of color, but rather with the difference between vision, of any kind, and complete blindness. Black differs as much as does white from the absence of all visual consciousness. In normal visual experience, difference in intensity is perhaps observable between the center and the periphery of the visual field, while "vision behind the head" is of zero intensity.

Other color attributes which are of importance in perceptual studies include the so-called "modes of appearance," or *Erscheinungsweisen.*[222] Thus, colors may appear as "body," "surface," or "film." They may also be lustrous or non-lustrous.

NOTE B. AUDITORY QUALITIES AND THEIR ATTRIBUTES.

145. *The Classification of Auditory Elements.* — Auditory experience may be defined or identified, by psychophysiological means, as consisting of those experiential aspects which exhibit a reliable correlation with the action of sound waves upon the ears. If both ears are entirely shielded from acoustic influence, auditory experience will normally be at a minimum, and when sound waves are aurally operative, the variations in such experience are closely determined by the character of the waves in question. Similar forms of experience, based upon *spontaneous* sense-organ activities or brain excitations may, of course, be observed, as in the case of vision.

If we study the aspects of experience which are thus delimited, a purely introspective analysis yields the following general results. Auditory experiences are normally complex, both coexistentially and in time; although the temporal aspect of auditory forms of combination is the more important, just as the spatial aspect predominates in vision. The proximate constituents of such experiences show a wide variety of qualities, which are rather difficult to classify, although some of them exhibit definite systematic similarities. The most outstanding subdivision is apparently that between *tones* and *noises*. The former furnish the fundamental materials for musical composition, whereas the latter are primarily non-musical. Intermediate between the purest tones and the purest noises, we find a great many qualitatively different auditory constituents, most prominent among which are so-called *vocables*. The latter are characteristic of the auditory representation of language. Among the vocables, the *vowels* are predominantly tonal, whereas the *consonants* are predominantly noisy. The majority of concrete musical tones, also, are *somewhat* noisy, and practically all noises have some tonal quality. The distinctions between these several classes of auditory qualities can only be appreciated by concrete exhibition in experience, although we may identify them by means of their psychophysical correlations, thus providing the information needed for staging an actual demonstration.

The components of auditory experience characteristically show varying degrees of *fusion*, so that a thoroughgoing description in terms of elements is seldom possible. Insofar as fusion actually exists, it is evidently illegitimate to report upon the experience in terms which are one hundred per cent analytical. However, as a rule, the " fusions " are not complete, the elements still being salient to some degree. Recognizing these facts, we may say that tones and noises are fundamental auditory elements, while vocables, clangs and other intermediates correspond to highly fused combinations of such elements, according to a wide variety of formulae. Observers differ greatly in their ability to analyze auditory experiences which have complex stimulus conditions.

146. *The Attributes of Tones.* — Tones[242] may be considered first, because they lend themselves to the construction of a continuous system much more readily than do vocables and noises. However, the tonal system appears to reveal properties which are characteristic, also, to some degree, of the other classes of auditory constituents. Musical scales involve the arrangement of tones in order of their attribute of *pitch*. This arrangement permits of a continuous series of tones, each just noticeably different from its neighbor, ranging from the lowest bass to the highest treble. In an independent dimen-

sion, perpendicularly to the pitch line, each tone can show many gradations of *loudness*, or of subjective intensity.

Under ordinary conditions, tones manifest two other introspectively discriminable attributes, which, however, are rather more difficult to identify and to define. These are known as *brightness* and *volume*, respectively, and they both show a very close correlation with pitch. Brightness (or shrillness) is contrasted with dullness or mellowness, and stands for a certain saliency of the tones, against the general auditory background. In the tonal system, it increases constantly as the pitch is raised, so that it can conveniently be combined with the latter to form a single dimension, known as pitch-brightness.[243] In other relationships, as in the comparison of tones with vowels, brightness varies independently of pitch. The attribute of volume should not be confused with that of loudness. It stands for an auditory extensity or expansiveness of the tone, which is large for low pitches and decreases progressively as the pitch increases. Although this extensity can hardly be translated into terms of visual space properties, it seems satisfactory to regard it as signifying the amount of *purely auditory space* which the tone occupies. The separation of volume from pitch in the tonal manifold is justified by the fact that, in terms of just-noticeable differences, it varies more slowly than the

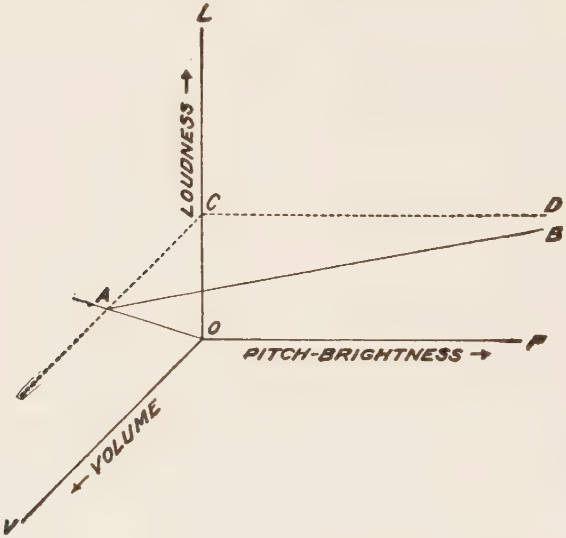


FIG. 9. COÖRDINATES OF THE TONAL MANIFOLD.

The diagram shows a set of three-dimensional Cartesian axes, for pitch-brightness, loudness and volume, respectively. Owing to the fact that volume varies as a function of pitch-brightness and of loudness, only a restricted number of points in this three-dimensional system represent possible tones. They are clustered around some such plane as *POAB*.

latter. It also varies independently of pitch in systems involving other auditory qualities.

Thus, it appears that we can represent the manifold of all pure tones by means of a three-dimensional figure, a solid, having the dimensions of pitch-brightness, loudness, and volume, respectively. (See Fig. 9.)

If we compare pitches amongst themselves, we find that they manifest periodic similarities and differences, along the pitch line. Pitches which are separated by the musical interval known as an octave, or by multiples of this interval, are said to be similar in octave quality. *Octave quality* may be compared with the psychological primacy of the hues, red, yellow, green, and blue in the color solid. Like the psychological primaries, it cannot be represented conveniently by a special dimension in the tonal manifold, but can be designated by means of a scale marked off on the pitch line. Another method is to consider the pitch line as describing a helix in a fourth dimension, so that the coils return to the same value of this dimension, measured in angular units, once every octave. Certain physiological considerations, to be presented later, suggest that the phenomenon of octave similarity is due to a latent complexity of constitution in the tones which exhibit it. Tones are also sometimes said to possess *vocalic quality*, which is defined by their degree of resemblance to particular vowels. However, it would appear that a more fitting way of formulating this resemblance would be to say that the vowels possess tonal or pitch quality, and to reserve the term, *vocality*, for the over-all quality of vowels, as such.

147. *The Properties of Noises.* — Noises are difficult to arrange into a continuous or quantitative system, except in the dimension of loudness. According to Titchener,[244] noises can be divided into two temporally distinguished classes, the explosive and the continuative. The former are exemplified by "crack," "pop," and "snap," and the latter by "hiss," "sputter," and "rumble." However, when carefully studied, noises show a possibility of arrangement in pitch order, as well as in terms of loudness. They also manifest variations in brightness and volume. Their own peculiar qualitative features have, thus far, eluded quantitative systematization from the purely introspective standpoint.

Pure tones are practically never realized even under conditions of laboratory experiments, and the combinations of tones and of noises which actually occur have characteristic qualities of their own. One of the most outstanding of these is *timbre* or "tone-color," which may be viewed as representing the combination of a number of systematically related tones; a given tone with its so-called over-tones. Differences in timbre are demonstrated in the divergences in quality between two different musical instruments, such as the cornet and piano, at the same fundamental pitch. In practice, the majority of musical instruments also involve characteristic noise components, such as that accompanying the scrape of the bow in the case of the violin. Vocality, or vowel quality, is another example of this sort of over-all qualitative distinctiveness of auditory combinations.

NOTE C. OLFACTORY QUALITIES AND THEIR CLASSIFICATION.

152. *Classifications of Odors.* — From the introspective standpoint, the olfactory qualities exhibit an astonishing variety. They are closely associated

with, and similar to, the gustatory or "taste" qualities, being confused constantly with the latter in everyday life. It is only by means of a psychophysiological criterion that we can separate these two classes of experiences with any degree of certainty. However, on a physiological basis, we can identify the olfactory qualities by excluding vaporous substances from the higher cavities of the nose or, more accurately, by noting what forms of consciousness are lost when the first cranial nerve is destroyed or anaesthetized.

Numerous attempts have been made to arrive at a satisfactory classification of the olfactory qualities from the introspective standpoint. Although some progress has been made, we are still unable to outline a system which is as definite and well-authenticated as are those which we have considered for visual and auditory experience. The most primitive division is that made by von Haller, into sweet, indifferent and foul odors, a classification which is evidently based upon the affective rather than upon the purely sensory aspects of the experiences. Although these affective aspects are highly characteristic of the system of odors, they are far from being invariable. A more sensory classification is that of Linné, who distinguished between the following species: aromatic, fragrant, ambrosial, alliaceous, hircine, repulsive, and nauseating. This system, as expanded by Zwaardemaker,[251] may be tabulated, with examples, as follows:

TABLE I

Zwaardemaker's Classification of Odors.

1. Ethereal	Odors of fruits, ethers, aldehydes, ketones, beeswax.
2. Aromatic	Odors of camphor, turpentine, ginger and other spices, lemon, nitrobenzol.
3. Balsamic	Odors of flowers, vanilla, and the like.
4. Ambrosial	Odors of amber and musk.
5. Alliaceous	Odors of hydrogen sulphide, rubber, chlorine, bromine.
6. Empyreumatic	Odors of roast coffee, tobacco smoke, benzol, and phenol.
7. Caprillac	Odors of cheese, rancid fat, cat's urine.
8. Repugnant	Odors of henbane, certain bugs.
9. Nauseating	Odors of faeces, decayed flesh, and the like.

153. *Henning's Olfactory Prism.* — Classifications such as these are based upon the relationships of similarity and difference between the multitude of distinct odors which can be realized in experience. The Zwaardemaker scheme suggests that the olfactory qualities fall into discrete classes, with no transitional members. However, common experience provides plenty of evidence that this is not the case, and it would seem that a careful study of all kinds of olfactory experience should reveal a qualitative continuum. Such a continuum has been proposed by Henning[252] in the form of a so-called *smell prism.* Henning bases his system upon the statements of individuals who have had a particularly wide experience in discriminating odors. He concludes that six primary reference points are sufficient to establish the system of olfactory qualities. These correspond to the following odors:

F = Fragrant (= flowery, *blumig*, or *duftend*)
E = Ethereal (= fruity, *früchtig*)
P = Putrid (= foul, *faulig*)

S = Spicy (= aromatic, *würzig*, *gewürzhaft*)
R = Resinous (= piny, balsamic, *harzig*, *balsamisch*)
B = Burned (= burning, scorched, empyreumatic, *brenzlich*)

These primary, or simplex, odors are placed upon the six respective corners of a triangular prism, in the manner shown in Fig. 11. The prism as being hollow, *i.e.*, qualities are supposed to be represented by points on its surface only, not within its volume. Points on the five faces of the prism must obviously stand for qualities which are intermediate between those placed upon the corners. Macdonald[253] designates the primary odors as simplex, those lying along an edge as duplex, those on the top and bottom faces as triplex, and those on vertical faces as quadruplex, or multiplex. Macdonald's experimental studies of the system indicate that it is an advance over previous schemes, but has serious logical difficulties in relation to characteristic stimuli. No odors were found for the triplex surfaces, and only one odor which could be interpreted as belonging to the EPBR face. Odors which are judged to be either duplex or triplex may occur in relations such that they must be placed upon quadrilateral faces.

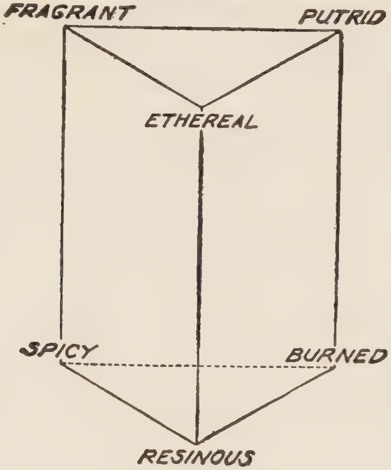


FIG. 11. THE OLFACTORY PRISM, ACCORDING TO HENNING.

The figure represents a prism, of triangular cross-section, with the six, supposedly primary, odors at the respective corners. Henning regards the prism as hollow, distinctive qualities being represented on the edges and faces only. However, variations in subjective intensity can be taken into account by viewing it as a solid.

As described by Henning, the olfactory prism provides no explicit representation of the intensity dimension. However, if the figure is regarded as solid, rather than as hollow, intensities can be symbolized by means of distances from a central point or locus measured in the direction of the surface point which represents the given quality.

NOTE D. GUSTATORY QUALITIES AND THEIR RELATIONSHIPS.

157. *The System of Gustatory Qualities.* — The separation of the gustatory perceptions from those which involve tactual, thermal, or algesic channels has been made possible only on the basis of psychophysiological studies, which show that the experiences — localized within the mouth and called sweet, salt, sour and bitter — are correlated with the stimulation of characteristic sense-organs, known as taste-buds. The four primary taste qualities vary separately in intensity, along a continuous scale. They readily show intermediates at low intensities, but at high intensities they tend to be mutually exclusive. Henning [254] has advocated the use of a tetrahedron to represent the system of gustatory qualities, the four primaries being placed at the four corners, respectively, as shown in Fig. 12. Intermediate qualities, or gustatory "mixtures," find positions on the edges and faces. According to Henning, the tetrahedron is to be regarded as hollow, but we can represent the intensity dimension by treating the figure as a solid and measuring intensities from a central point, in the direction of the surface point which symbolizes the given quality.

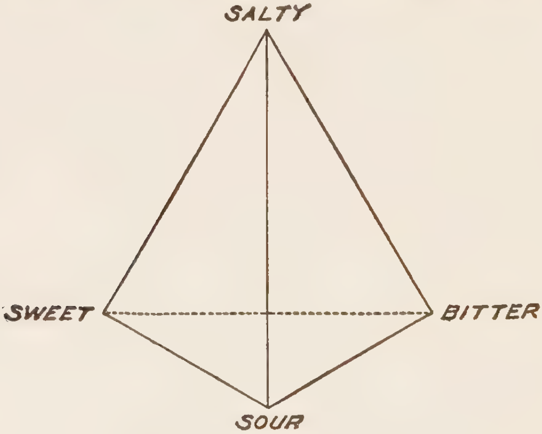


FIG. 12. THE GUSTATORY TETRAHEDRON, ACCORDING TO HENNING.

The figure represents a concatenation of four triangular surfaces, with the four elementary taste qualities at the respective corners. According to Henning, the structure is hollow, but it is best regarded as a solid.

NOTE E. THE CLASSIFICATION OF CONTACT QUALITIES.

156. *Psychological Basis of Analysis in this Field.* — We come now to deal with a group of perceptual relationships for which the object must ordinarily be in intimate proximity to the body surface, in order that it should

participate in the determination of consciousness. The sense channels which are involved in this case may be characterized as contact-receptive in contrast with distance-receptive. The subdivision of contact perception along sensory lines has offered many difficulties in the past and, even at the present day, cannot be regarded as complete. For example, we are unable to select, upon an objective basis, certain specific receptors in the skin and say that temperature experience consists in those psychical factors which are correlated with the functions of these particular end-organs. Instead, we are compelled to utilize the qualitative differences which we find directly within experience as the principal clues to our analysis. However, the introspective distinctions are substantiated by a few specific correlations which we can discover between the psychical differences and physiologically separable sense channels.

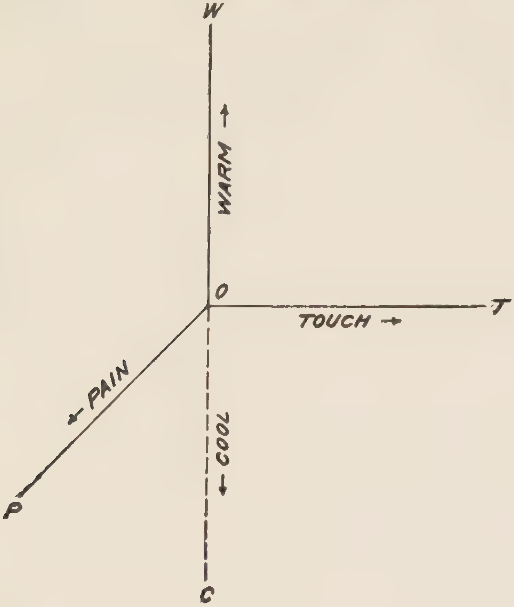


Fig. 13. The Manifold of Cutaneous Sensibility.

The diagram shows a set of three-dimensional Cartesian axes, for warm-cool, touch and pain, respectively. Warmth is measured positively from the point, *O*, and cool negatively from the same point.

After having established some of these analytical relationships, we usually feel impelled to say that the deliverances of the separate sensory systems *fuse* with one another. Thus, the taste of lemonade is said to be a combination of gustatory, olfactory, touch, and temperature sensations — although, to the naïve observer, it seems to be a simple qualitative experience. However, there is no actual *process* of fusion, within experience, but only a determination of the experiential resultant, simultaneously, by the operations of a plurality of sensory receptive mechanisms and nerve channels. The psychophysiologist is, of course, compelled to consider the nature and relationships of such resultant experiences, but in order that he should understand them, he must first become acquainted with the correlations between experience and the separate functioning of the individual afferent systems.

From the purely introspective standpoint, it is easy to divide contact experiences into those of taste, touch, temperature and pain. Each of these has a number of discriminable kinds. Thus, taste may be sweet, salt, sour or bitter; touch presents either neutral touch or tickle; temperature consists of warm or cool; while pain has various qualities, including itch. Intermediate or "fusion" qualities of all possible sorts are found between these primary contact experiences. They also shade into the distance-significant olfactory experiences, on the one hand, and bodily experiences, such as lust and kinaesthesis, on the other hand.

The non-gustatory qualities may be localized at almost any point on the experiential body surface, including zones extending some distance within either end of the alimentary canal. They are all qualitatively distinctive and are capable of independent variation in intensity. With certain exceptions, they may show all conceivable qualitative intermediaries, having either simple or complex relations with the primaries. Warm and cool are ordinarily mutually exclusive, but may be regarded as possessing an intermediate in the experience which is known as "hot." "Burning heat" also involves a similarity to pain.

The non-gustatory experiences may be represented by means of a three-dimensional diagram, such as that shown in Fig. 13, in which the thermal qualities are treated as algebraically related. This latter treatment evidently finds an exception in the case of "hot," which is excluded by the geometry of the diagram. In general, with this exception, any non-gustatory contact experience can be represented by a particular point in the given three-dimensional manifold.

NOTE F. THE ANALYSIS OF KINAESTHETIC EXPERIENCE.

163. *Classification of Kinaesthetic Experiences.* — The kinaesthetic experiences have to do with the position and movement of one's own body in space, and with postures and relative displacements of the parts of the body itself. It is convenient to divide these experiences into two classes: the *absolute* and the *relative*. The first class is concerned with the geometrical and kinematical relations between the body and its environment, while the second stands for the postures and relative movements of the bodily members. Each of these sets of facts can also be represented visually and, to some extent, tactually. It is very easy to eliminate the visual factors, apart from images, by closing the eyes; and the tactual ones can be avoided by the proper application of anaesthetics to the skin. The remaining representations are predominantly kinaesthetic.

Since the kinaesthetic impressions are concerned principally with forms and movements, rather than with differences of kind or degree, it is natural that they should be closely structured and difficult to break up into component qualities. Indeed, these experiences exemplify the principles of fusion and configured wholeness more radically than do any other conscious phenomena.

Consequently, their most significant aspects must be considered under the captions of composite and temporal perception. Nevertheless, it would certainly be incorrect to imply that they are wholly unanalyzable, or that they cannot be regarded at all as subjective mosaics of characteristic qualitative elements.

We can distinguish at least five component aspects of experience which belong in the kinaesthetic class. In the group of absolute kinaesthetic experiences, we have: (1) the kinaesthetic vertical and (2) dizziness or vertigo. In the group of relative kinaesthetic experiences, we can recognize: (3) attitudinal qualities (having to do with posture and bodily movement), (4) tensive (or weight-resistance) qualities, and (5) exertive (or muscular pressure) components. The first three of these modes of kinaesthetic experience are rather difficult to conceive apart from specific configurations. Thus, the concept of the vertical, even as defined introspectively, seems to imply a relationship between a number of spatial components. Dizziness, again, seems introspectively to be a movement, and hence to be characterized by directionality and change. It is not easy, moreover, to get a concrete impression of what is meant by an element of kinaesthetic attitude.

However, a more careful consideration of the actual subjective facts, as well as of the scientific system into which they must enter, will probably justify us in believing that these five factors correspond to qualitatively distinct experiential elements. We must have a combination of such elements, in the form of a fused spatial mosaic, in order to yield the kinaesthetic patterns which appear in concrete, everyday experience. Combinations of this sort may involve kinaesthetic components of the same species, or simultaneously of different species, or even definite concatenations of kinaesthetic with non-kinaesthetic factors. Concepts, such as those of the vertical and of rotation, which are relative from the standpoint of physics, are actually absolute subjectively. The introspective vertical can be regarded as a fixed qualitative constituent of consciousness, which is normally related in a certain way to other concomitant experiential factors. When these relations are disturbed, we designate the experience as that of a departure of the body from a vertical position. The vertical itself is thus not the product of a relationship, but is a reference axis with respect to which such relationships can be established. Although motion may necessarily be relative for physics, it is usually absolute for psychology, because certain portions of consciousness are accepted as being definitely "at rest."

NOTE G. INTERNAL EXPERIENCES AND THEIR PSYCHOPHYSIOLOGICAL RELATIONS.

168. *The Classification of Internal Perceptions.* — In addition to the qualitative experiential components which we have considered above, consciousness frequently contains characteristic qualities which can be correlated with specific metabolic conditions or processes of a non-motor sort, within the organism. These qualities may be treated as "internal sensations," from the standpoint of their stimulus-receptor conditions, or as "perceptions" in their relationships to the gross bodily states which are involved. It seems just as legitimate to regard hunger as perceptually related to a lack of appropriate food substances in the stomach, as to view sweetness, similarly, as being cor-

related with the presence of such materials in the mouth. The perceptual treatment is particularly indicated by our ignorance of the stimulus and receptor processes for the majority of these experiences.

One of the most satisfactory classifications which has been proposed for the experiences in question is that of Luciani and Magendi.[266] These authorities, however, include the kinaesthetic qualities which, on account of their distinctive relationship to motor conditions, seem worthy of a special category. The non-kinaesthetic internal qualities may accordingly be said to include: (1) desires, (2) gratifications, (3) fatigues, (4) illnesses, and (5) coenaesthesia. Although it is generally stated that these experiences are vague and difficult to analyze, they are nevertheless of the utmost psychological importance. They represent specific organic conditions which must exercise a regulative action over behavior if the organism or the species is to survive. Consequently, the internal experiences and their associated physiological processes are of paramount interest in connection with problems of *motivation*, which we shall consider at a later point in this work (see Volume III), and it is desirable that their psychophysiological relationships should be established as definitely as possible.

169. *Desires.* — Desires are forms of experience characterized subjectively by an attribute which may be given the name of *urgency*. This attribute is associated with volitional unrest. Although desires may sometimes occur at low intensities, they are capable of becoming very powerful, and may dominate consciousness completely if they are not satisfied. The principal experiences in this class are: (1) hunger, (2) thirst, (3) lust, (4) the desire to micturate, (5) the desire to defecate, (6) the desire for air, and (7) in the case of the female, under appropriate conditions, the desire to lactate. There is also a special kinaesthetic state, popularly known as "nervousness," which may be interpreted as a desire for activity or "a change." These names may be understood as designating subjective qualities, although it is necessary to include the objective conditions in the meanings of some of them. The desiderative experiences have configurational aspects, but the latter are apparently subordinate in significance to the qualitative nature of the experiences, apart from their localizations or patterns. Consequently, we can discuss them quite adequately under the present caption of "component perception." Unfortunately, there will be little that we can add to this perceptual treatment when we come to the chapters on sensation.

Hunger. — It is a familiar idea, of course, that the *hunger experience* is correlated with a need for food on the part of the organism. However, this conception is by no means an accurate one. Hunger usually appears far in advance of any serious metabolic deficit and, on the other hand, it may disappear entirely in the presence of a fatal nutritive failure. The investigations of Cannon [267] and of Carlson have made it clear that the characteristic hunger feeling is determined by the contractions of the stomach, which begin, as a rule, four or five hours after this organ has emptied itself. A "hunger pang" goes with each single gastric contraction. However, it is necessary for the walls of the stomach to be in a special physical or chemical condition in order that this relationship should obtain. Gastric movements which occur during the digestion of food have an entirely different representation in consciousness. Under starvation, hunger disappears in about two days, although, according to Carlson,[268] the stomach movements may continue. Hence, we may regard hunger as the perception of gastric contractions in the presence of a condition of the stomach walls which is transitional between that of the normal digestive process and the state of starvation.

The function of hunger is obviously to prevent the incidence of the latter state. Nothing is known concerning the quantitative relationships of the hunger experience and its organic conditions; presumably the mechanism which is involved is similar to that of muscular pain.

Thirst. — The thirst experience introspectively resembles a complex of tactual qualities, being a feeling of dryness and heat in the throat. It can evidently be attributed to a reduction in the amount of water in the body tissues, particularly in those of the pharynx. Thirst is more persistent than is hunger, in fasting, but is said finally to disappear. It is common knowledge that thirst can be aroused by eating substances, such as spices and salt, which have a tendency to abstract water from the tissue cells.

Lust. — Sexual desire, or lust, includes a group of experience components which have the common attribute of voluptuousness. We may distinguish, however, between a low intensity feeling of erotic irritation — which may be unpleasant — and higher intensities which are characterized by extreme pleasantness. The orgasmic experience, which constitutes erotic gratification, seems to differ from the preliminary feeling of desire only in its localization and intensity. Experiments have shown that in lower animals, such as the frog, sexual response depends upon pressure between the contents of the seminal vesicles and their walls. However, in the human instance, this seems to be a relatively unimportant feature, since erotic desire is practically independent of periodicity in the reproductive processes and may persist after repeated gratification.

It is apparent that, in man, the sexual process has been given a powerful support in the central nervous system, which liberates it to a large degree from organic stimulus conditions, and connects it more with environmental factors. Thus, sexual desire in man should perhaps be regarded as part of the perception of a sexual object. Nevertheless, from our present standpoint, lust can be viewed as being perceptually determined, to a very important degree, by the state of tumescence of the external genitalia. It is true, of course, that the intensity of the desire is not reliably proportional to the degree of such tumescence, but the intensity is related to the approximation of the physiological condition to that required for ejaculation. However, it would probably be found impossible to specify this condition in non-neurological terms.

Excretory and Secretory Desires. — The *desire to micturate* is ordinarily said to be due to fullness of the bladder. However, it appears that this experience must actually be referred to the magnitude of the pressure between the bladder walls and the contents; and such pressure may arise either from passive distention of the organ or from its active contraction. The latter condition may accompany emotional states such as those of fear or "nervousness." Hence we may view the micturitional experience as a perception of intravesicular pressure.

The *desire to defecate* is to be attributed to the presence of fecal or other matter in the large intestine. It seems impossible to account for the differences in quality between the micturitional and defecatory experiences by means of composition in terms of simpler components. The *desire to lactate* is evidently determined by an excessive pressure of milk within the mammary glands.

The Desire for Air. — The experiences which accompany suffocation are of a very characteristic sort, although uncommon in everyday life. They are probably to be attributed to interference with the normal operation of the respiratory apparatus, rather than to a lack of oxygen or to an excess of carbon dioxide in the blood. The breathing of air which is low in oxygen may result in syncope without respiratory distress; but noxious vapors may bring about an inhibition of the reflexes and produce an effect similar to that due to physical obstruction of the movements.

General unrest or the so-called feeling of "nervousness" will probably require explanation primarily in terms of central factors. It may be due to enforced inactivity or to the associative arousal of desiderative forces, related to those which we have already discussed above.

170. *Gratifications and Fatigues.* — *Gratifications.* — The release of the organism from the conditions which give rise to desires, yields characteristic experiences. In some cases, the gratifications are similar in quality to the corresponding desires, involving a marked increase in intensity which is followed by a lapse of the given kind of experience altogether. This is the case with lust, micturitional and defecatory desires. The relation of these gratifications to organic processes is very familiar. The sexual orgasm, considered as an experience, is, perhaps, to be attributed perceptually to the muscular contractions which occur in both the male and female organs, although central conditions are undoubtedly involved in a very important way. It is probable that in the cases of micturition and defecation the movements of the excreted materials through the urethra and colon, respectively, furnish the primary condition.

The gratification of hunger involves not only the disappearance of the original experience but its replacement by a sense of gastric fullness, corresponding to the distention of the stomach by food and the beginning of digestive activity. Thirst is gratified by the contact of liquids with the dry membranes of the back of the mouth, with an accompanying coolness and wetness.

Fatigues. — Fatigue experiences exist in numerous qualitative varieties. Muscular fatigue is rather definitely localized and passes over into a pain quality at high intensities. It may be attributed to an excessive breakdown of muscular tissue through work or, possibly, to an accumulation of end-products of the chemical activity in the muscular tissue. General fatigue is a more diffuse experience which does not resemble pain, although it is commonly unpleasant. It is probably due to an abnormal concentration of metabolic end-products in the blood stream. Drowsiness or sleepiness has a similar basis in the direct action of these substances upon the cells of the cortex. We can scarcely classify this latter relationship as perceptual.

The feelings of satisfaction or of satiety which follow erotic gratification or the ingestion of a full meal are grouped by Luciani with fatigue. These feelings are distinct in quality from those which characterize desire and gratification in the respective fields. However, they are rather closely similar for the erotic, micturitional and defecatory cases. These experiences are perhaps to be assigned to the reduction of tension or activity in the given fields below that which is normal or average. The similarity of these feelings to those which go with convalescence from illness suggests the use of the term, *analepsis*,[269] to stand for them.

171. *Specific Illness Perceptions, and Coenaesthesia.* — In addition to the types of experience which go with the healthy life of the organism, we must also deal with those which accompany pathological conditions. There is a great variety of qualitatively distinct illness qualities. The majority of these

must be classed, introspectively, as pains, although differing in quality from cutaneous pain, and among themselves. However, a distinctive feeling such as nausea can scarcely be regarded as a pain, in spite of its great unpleasantness.

Practically every internal organ seems to be capable of yielding a characteristic pain under appropriate conditions, although many of these organs are insensitive to mechanical or thermal stimulation, so that in surgical operations they can be cut or burned without any corresponding modifications of consciousness. However, the external peritoneum, the lining of the abdominal and pelvic walls, yields pain upon mechanical stimulation, while the tissues of the diaphragm may be stimulated mechanically to give pressure experiences, as well as those of pain. Other internal parts can yield pressure feelings under appropriate conditions. These conditions probably involve changes in the physical or chemical states of the tissues, just as in the case of the stomach walls or a rheumatic muscle. Pain or pressure may then arise either in consequence of these changes *per se*, or under the added influence of mechanical forces.

The differences which exist between internal pains will readily be appreciated from a few examples, such as headache, toothache, colic pains, pain due to cramp in the muscles of the rectum, bruising the testicles, etc. Each one of these algesic experiences has a specific organic condition, so that the experience may be said to be a perception of the condition in question. However, our knowledge of the physiological or physical nature of such conditions is very meager. Presumably, headache is to be referred to pressure between the brain and the cranium, which compresses the meninges, the volume of the brain varying with the pulse pressure to give the characteristic throbbing. Toothache stands for decay, or chemical or thermal abnormalities in the tooth substance. Muscular pain may represent cramp, or excessive contraction of the muscular tissue; extreme concentration of metabolic end-products; or damage to the cells due to overwork. Colic pressures or pains are said to be due to pressure of the distended small intestine upon the peritoneum.[270]

Nausea is undoubtedly a complex experience, but has a characteristic quality which furnishes its central nucleus. Its foundation may lie either in the presence, in the stomach, of materials which are unsuitable for food, or to the reflexly induced reactions which tend to expel these substances. Owing to the commonness of nausea in connection with illnesses or emotional disturbances which do not have a digestive basis, the latter assumption seems to be most plausible. In this case, the essential experience must be regarded as a perception of the activity of those muscles which are primarily concerned in vomiting.

Coenaesthesia. — The term, coenaesthesia, is ordinarily used to stand for a general mass of experience which constantly represents the organism in its healthy state. As defined by Henle,[271] this presumably includes kinaesthetic factors. Under ordinary conditions, the experience lies in the margin of the conscious field, furnishing a constant background, against which other impressions are projected. However, in a state of especial organic vigor or "pep," the coenaesthetic factor may assume a high degree of clearness and intensity, constituting a perception of well-being or euphoria. This experience also appears, as an hallucination, in certain diseased states, such as paresis. The disappearance of the normal coenaesthesia under other pathological conditions, sometimes causes the patient to judge that his ego or personality has been obliterated.

PATTERNS OF ORGANIC EXPERIENCE

It is evident that the various types of internal or organic experience have special distributions within the experiential corporeal field. When these particular qualities arise, they are almost always localized in a fairly definite manner. Thus, hunger is felt in the region of the stomach, lust in the sex organs, the micturitional sensation in the urethra, etc. The general feeling of well-being, or coenaesthesia, tends to permeate the bodily complex as a whole, although sometimes it is more concentrated in some portions than in others. The experiential distribution of these qualities is a function of the location of the corresponding organic conditions within the physical body. However, it is an interesting fact that the subjective and objective distributions do not necessarily resemble each other closely. Thus, the localization of the desire to micturate, in the urethra or the genitalia, does not correspond with the physiological fact that the conditions which give rise to these feelings are situated in the bladder.

194. "*Referred Pain.*" — The facts of "referred pain" are further illustrations of this point. Head and others[294] have made very elaborate studies, showing how disturbances of the internal organs yield pains, localized on the periphery of the body in definite zones, the identity of which is determined by the location of the organic disturbance in question. Thus, cardiac troubles elicit pains in the neck, shoulders and back; bladder troubles may evoke pains in the back of the legs, and so on. Head has formulated a law of the false localization of internal pains, according to which "when a painful stimulus is applied to a part of low sensibility in close central connection with a part of much greater sensibility, the pain produced is felt in the part of higher sensibility rather than in the part of lower sensibility to which the stimulus was actually applied." It is to be noted that in spite of the lack of similarity between the subjective and the objective locations, or bodily patterns, in this situation, the two configurations are nevertheless functions of each other. It is, of course, upon this fact that the diagnostic utility of referred pains is based.

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INDEX

A

Aberration, chromatic, 106, 116
  chromatic, of eye, 183, 186
  optical, 106–107, 116
  spherical, 116
Abney, W. de W., 91, 94, 163, 166, 182, 193
Abraham, O., 223, 236
Absorption, selective, 65
  selective, in eye, 183, 184
Acceleration, sense of, 333–334
Accommodation, 99
Action current, of nerve, 18
Action time, for brilliance, 89
Acuity, chromatic, 176, 190
  intensity law, 86, 119
  intensity law, retinal basis of, 132–134
  visual, 85–87, 115–116
Adaptation, auditory, 238
  bright, 125
  chromatic, 178–182, 193–195
  dark, 123–124
  equations for, 124–125
  gustatory, 288–290
  olfactory, 273, 274
  photopic, 93–96, 123–126
  scotopic, 96–97, 123–126
  tactual, 317
  tensive, 343
  thermal, 301, 302, 305
Adrian, E. D., 16, 32, 35, 41, 42, 49, 127, 130, 318, 320, 321, 322, 323, 327, 346, 347, 350
Afferent arc, analysis of, 8–14
Afferent conduction, 8–9, 12–13
Afferent nerve excitation, 8, 12
After-effects, auditory, 238
After-image, complementary, 180–181
  of Purkinje, 91, 120
After-images, negative, 93, 95, 97
  positive, 90–91
  tactual, 317
After-tones, primary, 238
Air, desire for, 366, 367–368
Alkaloids, 282, 284, 294
All-or-none law, 16, 254
  in nerve, 35–37
Allen, F., 55, 182, 189, 204, 237, 288, 289
Allers, R., 342, 343
Alsberg, 302
Ampullae, 331–332
Anaesthetization, faradic, 340
Analepsis, 368
Analysis, auditory, 210, 255–256, 259
  sensory, 3–6
Angles, visual, 106
Antagonism, between warmth and cold, 310–311
  olfactory, 267–268
Aristotle's illusion, 322
Aronsohn, E., 262, 274, 280
Articular sense, 339–342
Asparagine, 292
Astigmatism, 100, 106, 116
Attributes, 2, 3
  chromatic, 353
Aubert, H., 77
Audibility curve, 211–214, 249
Audition, neurological relationships of, 254–260
  theories of, 244–245
Auditory composition, as function of frequency, 230
  as function of intensity, 230
  as function of stimulus complexity, 230–234
Auditory elements, 357
Auditory qualities, 357–359
Auditory quality, neural foundations of, 256
Auditory sensation, composite, 206–229, 229–235
  temporal 235–240
Auxesis, visual, 94

B

Baird, J. W., 173
Basilar membrane, 242, 243, 246, 247, 251
Basillary response, theories of, 244–245
Beats, auditory, 231–232, 238, 252
  subjective, 239
Bernhardt, 325
Bernstein, J., 321
Bezold-Brücke effect, 169–170, 173, 180, 182
Bills, M. A., 89, 177
Binocular sensory relationships, 202–205
Bipolar cells, of retina, 101
Bitonal stimuli, sensory effects of, 233
Bitterness, 282–283, 293–294, 362
Black, 192
Black body curves, 64
Blanchard, J., 77
Blind spot, 101
Blood vessels, retinal, 114
Blue arc phenomenon, 130–131
Borak, J., 342, 343
Boring, E. G., 260, 298
Bovie, W. J., 130
Brightness, 62
  auditory, 223, 357
  auditory, neural foundations of, 259–260
  auditory, basillary relations of, 248
  discrimination, visual, 76–80
  discrimination, visual and surroundings, 79–80
Brilliance, 54, 352
  absolute threshold, 75–76, 111
  action time of, 89
  and wave-length composition, 80–81
  as function of intensity, 75–81, 110–112
  as function of space, 81–84, 112–113
  as function of wave-length, 66–74, 108–110
  decay curve of, 89–90
  discrimination, as function of color difference, 74
  equations of, 68
  Fechner's law for, 76, 80
  field functions, 81–82, 115
  growth of, 89
  monocular neurological relations of, 116–139
  monocular refractive relations of, 97–116
  pattern functions, 83–84, 87, 115
  relative threshold, 78
  representation in nerve current, 130–132
  sensitivity for, 93–95
  stimulus relationships of, 66–97
  threshold, and retinal position, 81–82
  threshold, and size, 82–83
  time functions, 87–97, 116, 137–139
  time threshold, 88
  Weber's law for, 76–80
Broca, A., 89, 179
Brodhun, E., 77, 126
Browns, 175
Brückner, A., 177
Bull, O., 173
Bunsen-Roscoe Principle, in vision, 122–123
Burnett, N. C., 302

C

Campbell, C. J., 347
Candle, as photometric standard, 74
Carbon dioxide, in nerve, 27, 33–34
Carr, H., 298
Chaffee, E. L., 130
Charpentier, A., 90, 172
Charpentier's bands, 89–90, 138–139
Chemical senses, the, 261–295
Chords, 235
Choroid coat, of eye, 98
Chroma, 139, 150, 352
  areal functions, 172
  as function of intensity, 167–172
  as function of position, 196
  as function of space, 172–176
  as function of time, 176–182, 187
  as function of wave-length, 140–149
  as function of wave-length composition, 149–166
  -brilliance coefficients, 166
  decay of, 176–178
  field functions, 173
  monocular neurological relations of, 187–202
  monocular refractive relations of, 182–187
  monocular stimulus relations of, 139–182

  pattern functions, 174–176
  rise of, 176–178
  scale, spectral, 142–147
  spatial effects on, 186–187
Chromas, complementary, 151, 153, 154
  spectral, 140–147
Chromatic flicker, 178
Chromatic threshold, relative, 149
Chromatic time threshold, 177
Chromatic valence, 157
Chronaxy, 29, 38, 278
Ciaccio, 346
Clangs, 234–235
Clearness, 2
Cobb, P. W., 80
Cocaine, 290
Cochlea, 243
Coefficient law, 94
Coefficients, chroma-brilliance, 166
Coenaesthesia, 368, 369
Cold, paradoxical, 299
  receptor process for, 309–310
  receptors, 308, 310
  spots, 303
Color, achromatic, 352
Color blindness, 146, 164–165, 195–197
  total, 165
Color, chromatic, 352–353
  circle, 353
  cycle, 141
  definition of, 351
  excitation curves, 191
  introspective analysis of, 351–356
  modes of appearance of, 356
  names, 140–142
  sensation, problems of, 53–55
  solid, boundaries of, 356
  solid, psychological, 354
  space, 354–355
  spectrum, 141
Color-mixture, 150–167
  binocular, 203–204
  intraocular influences on, 185
  photometric aspects, 165–166
  theory of, 197
  three-component, 155–167
  two-component, 150–155
Color theory, Hering, 188, 197–200
  Ladd-Franklin, 188, 192, 200–202
  Young-Helmholtz, 188, 189–197
Color vision, abnormal, 164–165
  peripheral, 173–174
Color vision, theories of, 187–189
Colors, complementary, 193
  flight of, 181
  time relations of, 177
Combinational tones, 222, 231, 246–247
Complementaries, 151, 153, 154
  spectral, 154, 185
Complementary colors, 151, 153, 154
Composition, auditory, as function of frequency, 230
Conduction, afferent, 8–9, 12–13
Cone-cells, of retina, 101–104
Cones, retinal, 101–104, 117, 188
Consonance, 235
Consonants, 226–229, 357
Contact receptors, 14
Contrast, brilliance, 83–84, 132
  chromatic, 174–176, 195–196
  color, 174–176
  gustatory, 287
  retinal causes of, 136–137
Cornea, of eye, 98
Corpuscles, Dogiel's, 308
  Golgi-Mazzoni, 308
  Meissner's, 306
  Pacinian, 306, 308
  Ruffini's, 308
Corresponding points, 203
Corti, organ of, 243–244
Cosmic rays, 61
Crista acoustica, 331–332
Critical frequency, in gustation, 288
Culler, E. A. K., 301, 302
Current of rest, 18
Cutaneous sense, algesic, 296
  deep sensibility, 296
  epicritic, 296–297
  protopathic, 296, 297
  tactual, 296
  thermal, 296
Cutaneous senses, 296–328
Cutaneous sensibility, manifold of, 363

D

Dallenbach, K. M., 302
Davies, H. M., 298
Davis, H., 37
Deaf-mutism, 329
Deafness, 214
Decrement, transitional, 37

Decremental conduction, in nerve, 35–36, 46
Defecation, 366, 367
Depolarization, in nerve action, 22–24
Depth, visual, 52
Descartes, R., 16
Desires, 366, 367–368
Deuteranopia, 196, 199
Dichromatic vision, 146, 162, 164, 196, 199
Dieterici, C., 193
Difference tones, 232, 252
Diffraction, in eye, 183
Diffusion circles, 107
Diffusivity, visual, 137–138, 177, 187, 194
Dimming effect, 199
  achromatic, 95–96
  chromatic, 181
Dimmick, F. L., 272, 279
Discrimination, wave-length, 193
Dissonance, 235
Distance receptors, 14
Distortion, non-linear, 246, 251
Distortions, visual, 113
Distribution curves, auditory, 207–208
Dittmers, F., 80
Dizziness, 365
Dogiel's corpuscles, 308
Dominant wave-length, 140
Donders, F. C., 172
Dreher, E., 173
DuBois-Reymond's law, 29–30, 131
Duchenne, G. B., 340
Duplexity theory, 117–121
Duration, 2

E

E-substance, 50
Ear, inner, dynamics of, 245–247
  mechanism of, 241–244
  structure of, 241–244
Edridge-Green, F. W., 189
Einstein, A., 57
Electrical double layer, 21
Electrical stimulation, 326
Electrotonus, 29–30, 47
Elements, mental, 2
Empiricism, 7–8
End-bulb, Krause's, 306, 307, 308
Energy, acoustic, 209
  minimal for vision, 75–76
  radiant, 56
  threshold, visual, 83
Entoptic effects, 107–108, 114, 187
Equilibrium, visual, 88, 125
Erdman, E., 265
Erlanger, J., 38–39
Euphoria, 369
Ewald, T. R., 244
Excitation, nerve, mechanism of, 21–24
  nerve, recovery from, 31–32
Exertive sense, 346
Exner, F., 171
Experience, departments of, 13
Exposure threshold, 88
Exteroceptors, 13–14
Eye, anatomy of, 97–105
  dioptric parts of, 99–100
  dioptric power of, 99
  optics of, 105–107
  "speed" of, 100

F

Farnsworth, P. R., 223
Fatigue, retinal, 94
Fatigues, 368
Fechner, G. T., 55, 80, 302, 319
Fechner function, 76–80, 88, 112, 126, 132, 194, 214–216, 219–222, 224, 225, 349
Fechner-Holmholtz law, 94
Fechner's colors, 176–177, 187
Fechner's law, 349
  for brilliance, 76–80, 88, 112, 126, 132
  for noise, 225
  for pitch, 219–222
  in audition, 214–216
  in vision, 194
Fechner's paradox, 203, 204
Fenestra ovalis, 241
Fenestra rotunda, 242
Fischer, E., 226
Fixation, visual, 105
Fletcher, H., 213, 216, 221, 223, 256
Flicker, 71
  binocular, 204–205
  brilliance, 91–93
  chromatic, 178, 199
  critical frequency, 91, 92, 119, 138
  frequency, critical, 204–205
  photometry, 74, 138, 149, 179
Flourens, P., 335

Fluorescence, in eye, 183, 184
Fluttering-heart illusion, 120
Forbes, A., 16, 37, 46, 346, 347
Forbes, W. J. M., 199
Force, lines of, 57
Formants, of vowels, 228
Fourier analysis, in acoustics, 225
Fovea centralis, 104, 114
Francke, G., 262
Franklin, B., 57
Frequency, nerve impulse, 255, 257, 295
  neural, 18, 37, 40, 347
Fröhlich, F. W., 91, 112
Fusion, auditory, 229, 234–235, 357
  auditory, basillary basis of, 252–253
  visual, 91–93

G

Gamma rays, 61
Gasser, H. S., 38–39
Gault, R. H., 316
Gestalt, 3
Gley, E., 284
Goldscheider, A., 325, 328, 339, 340, 341
Golgi-Mazzoni corpuscles, 308
Golgi-organs, 345, 346
Gratifications, 368
Gravity, sense of, 330
Gray, A. A., 192, 244
Guareschi, 294
Gustation, persistence curves, 289
  receptor process, 290–294, 295
  selective changes in, 288, 290
  spatial relations of, 285–287
  successive contrast in, 288–290
  temporal relations of, 287–290
Gustatory intensity as function of stimulus, 283–287
Gustatory membranes, structure of, 292
Gustatory quality, as function of stimulus, 281–283
  neurological correlations of, 294–295
Gustatory tetrahedron, Henning's, 362
Gymnemic acid, 290

H

Haidinger's polarization brushes, 187
Hair-cells, auditory, 244, 247
Hair, nerve plexus of, 306
Haller, von, 360
Halos, chromatic, 187
Halverson, H. M., 224
Hänig, B. P., 286, 287, 291
Harmonics, subjective, 222, 230, 246, 247, 252, 258
Hartridge, H., 116, 186, 190
Haycraft, J. B., 282
Head, H., 296–299, 344, 370
Headache, 369
Head's theory of cutaneous sensibility, 296–297
  criticisms of, 297–299
Heat in nerve action, 33–34
"Heat," sensation of, 302
Hecht, S., 40, 69, 73, 86, 111, 116, 117, 118
Hecht, visual theories of, 121–136, 201
Helmholtz, H. von, 79, 99, 117, 136, 154, 177, 193, 244
  theory of accommodation, 99
  theory of color vision, 117
  theory of vowels, 226
Hemeralopia, 96
Henle, F. G. J., 369
Henning, H., 265, 270, 271, 279, 360, 362
  olfactory system of, 270–271
Hensen, V., 314
Hering, E., 94, 117, 179, 185, 308
  color theory of, 117, 188, 197–200
Hertzian waves, 61
Hess, C., 83, 84, 90, 173
Heterochronism, of nerves, 48
Heymans, G., 288
Hill, A. V., 22, 29
Höber, R., 283, 285
Hollingworth, H. L., 8
Hooke's law, 246
Hue, 54, 353
  as function of intensity, 169–172
  intraocular influences on, 183–184
Hues, psychologically primary, 192, 355, 356
Humor, aqueous, of eye, 99
Hunger, 366–367
Hyperexcitability, in nerve, 32
Hypermetropia, 100

I

I-substance, 50
Idioretinal light, 75–79, 129, 195
Illness, feelings in, 368–369

Illuminating Engineering Society, 69
Illumination, 62
Image, retinal, 56, 107–108
Images *vs.* sensations, 4
Inhibition, neural, 49
  Wedensky, 50
Inner ear, and kinaesthesis, 334–335
  proprioceptive organs of, 330–333
Intensity, 2
  acoustic, 207–209
  general basis of, 349
  of radiant energy, 59, 60–63
  of visual stimulus, 62–63
Interference, neural, 49
Intermediate tone, 231–232, 239, 252
Interoceptors, 13–14
Interruption frequencies, critical, for tones, 237
Interval, photochromatic, 167
Invariables, in spectrum, 170–171
Ionization, in nerve, 19–21
Irradiation, 87
  of pain, 326
Isochronism, of nerves, 48
Itch, 325, 328
Iterative nerves, 49
Ives, H. E., 92, 137–138, 161, 162, 177, 178, 187

J

James, William, 6
Joints, 338
Jones, L. A., 142, 147, 149, 184
Juhász, A., 279

K

Karwoski, T., 176, 182
Kato, G., 36
Katz, D., 323
Kiesow, F., 283, 285, 286, 287, 291, 315, 316, 317
Kinaesthesis, absolute, neural relations of, 335–336
  attitudinal, 338, 339–342, 365
  exertive, 337, 344, 365
  introspective analysis of, 364–365
  relative, neural relations of, 347
  tensive, 337, 342–344, 365
Kinaesthetic organs, mechanism of, 330–334
  sensation, absolute, 329–336
  sensation, relative, 336–348
  vertical, 103
Kirsch, R., 177
Kirschmann, A., 174, 175
Knudsen, V. O., 219, 221
Köhler, W., 17, 226, 228, 229
Kohnstamm, phenomenon of, 343
König, A., 77, 79, 85, 126, 136, 142, 161, 162, 163, 193, 352
Krause, W., 105, 307
Kucharski, T., 238
Kulpe, O., 352

L

Labyrinth, membranous, 330
Lactation, desire for, 366
Ladd-Franklin, C., 117
  color theory, 117, 188, 192, 200–202
Lane, C. E., 217, 232, 233, 244, 248, 250, 251
Langford, C. H., 94, 171, 180
Langmuir, I., 277
Lapicque, L., 22, 29, 38, 48
Lasareff, P., 121, 123
Lashley, K. S., 340
Latent period, tactual, 316
  visual, 89
Laurens, H., 142
Legendre, R., 38
Lens, of eye, 99
Lewinski, L., 339, 341
Light, 56
  definition of, 71–74
  mechanical equivalent of, 73
Lillie, R. S., 16, 22, 24, 27
Linné, 360
Localization, auditory, 214
  tactual, 322
Loudness, acoustic, 209–210
  as function of frequency, 210–214
  as function of frequency composition, 216–219
  as function of intensity, 214–216
  basillary relations of, 247–248
  laws of, 249
  neural correlate of, 256–257
Lowry, E. M., 147, 149, 184
Lucas, K., 16, 35, 40
Luciani, L., 308, 336, 339, 366, 368
Lumen, 62, 72
Luminosities, additive law of, 80
Luminosity curves, 68

Lussana, F., 336
Lust, 366, 367

M

MacDonald, M. K., 271, 361
Macula acoustica, 332
Macula lutea, 105, 185
Magendi, F., 366
Masking, auditory, 217–219, 250
Matthews, R., 127, 130
Mayer, A. M., 217, 219, 237
McDougall, W., 8, 16, 89, 139
McKendrick, J. G., 244
Meissner's corpuscles, 318
Membrane, of nerve, 19–21
Meyer, M., 244, 257
Micturation, desire for, 366, 367
Miller, D. C., 208, 209, 227, 228, 248
Millikan, R., 61
Millilambert, 62
Millimicron, 60–61
Minuthesis, visual, 94
Mixture, olfactory, 267–268, 272
Mixtures, gustatory, 283
Modulation, nerve current, 200–201
Monochromatic vision, 165
Movement, voluntary, 341
Muscle spindles, 345
Muscles, 338
  ciliary, 99
Music, 239–240
Myopia, 99

N

Narcosis, at synapses, 46
  in nerve, 24, 35–36, 46
Nasal passages, human, 265
Nausea, 369
Nernst, W., 16, 22
Nernst-Lillie, nerve theory, 16, 47
Nerve action, energetics of, 33–35
Nerve, auditory, 255
Nerve cell, resting state, 18
Nerve, chemical stimulation of, 24
  current intensity, 40–41
  electrical stimulation of, 22–23
  -ends, free, 326–327
Nerve excitation, fuel for, 33–34
  heat in, 33–34
  increased permeability during, 26–27
  resistance to, 27–29
Nerve excitation, thermodynamics of, 34
Nerve, fatigability of, 34
Nerve impulse, auditory, 254–260
  nature of, 18
  velocity of, 38–39
Nerve, mechanical stimulation of, 24
Nerve membrane, mechanism of, 20–30
Nerve, optic, 100–101
Nerve physiology, present status of, 15–16
  theories in, 16–18
Nerve processes, physical nature of, 15–50
Night-blindness, 96
  of fovea, 119
Nodal point, of eye, 105
Noise, 357
  basillary basis of, 253
  neural conditions of, 258
  pitch of, 225
  properties of, 359
  stimuli, 224
  stimulus relationships, 225–226,
Nothnagel, H., 301, 302
Nutting, P. G., 72, 79, 109, 216

O

Octave quality, 253, 359
Ocular media, absorption curve of, 109
Odors, classification of, 359–362
  duplex, 271, 361
  Henning's classification, 360–361
  multiplex, 271, 361
  simplex, 271, 361
  Zwaardemaker's classification, 360
Oehrwall, H., 286, 288
Ogden, R. M., 3, 5, 223, 229, 248, 259
Ohm's law, in audition, 222, 231, 251, 254
Olfaction, absolute sensitivity of, 266–267
Olfactometry, 266–267
Olfactory intensity, as function of stimulus, 263–268
Olfactory qualities, classification of, 359–362
  as function of stimulus, 267–272
  neural basis of, 278–280
Olfactory receptor process, 275–278
Olfactory sensation, temporal relationships of, 272–274

Olfactory stimulation, adsorption hypothesis of, 276–280
Optic nerve, excitation mechanism of, 126–127
Optical Society of America, 69
Ora serrata, 98
Organic compounds, olfactory relations of, 264–265
Organic series, and olfaction, 265–266, 269
Orientation, sense of, 329
Ossicles, of ear, 241–242
Otoliths, 332, 333
Oxygen, in nerve action, 33–34

P

Pacinian corpuscles, 308, 345, 346
Pain, 363, 369
  as function of stimulus, 324–326
  end organs of, 306
  neurological correlations of, 328
  referred, 370
  sensation, composite, 326
  sensation, cutaneous, 323–328
  spinal paths for, 328
  temporal correlations of, 325
Papillae, of tongue, 286, 291
Paradoxical cold, 301, 302, 310
Passy, J., 267
Pattie, R., 238
Paulsen, E., 262
Penzoldt, F., 266
Periodic table, olfactory relations of, 264
Permeability, of nerve membrane, 19, 24
Persistence of sensation, tactual, 317
  thermal, 305
Pflüger, E., 324
Pflüger's laws, for nerve, 22
Photochemistry of retina, 121–130
Photochromatic interval, 167, 172
Photometric measures, 56
Photometry, 62–63
  heterochromatic, 74
Photon, 63, 110
Photopic vision, 70, 118
Physiological zero, 299, 305
Piéron, H., 83, 89, 137
Pigmentary epithelium, 101
Pillsbury, W. B., 339, 340
Pitch, 211, 357
  as function of frequency, 219–222
  as function of frequency composition, 222–223
  as function of intensity, 222
  basillary relations of, 247
  -brightness, 358
  dominant, 234
  laws of, 250–252
  of clangs, 223
Place-theory, auditory, 254
Planck's law, 64
Polarization, in nerve, 21, 24
Pollock, L. J., 298
Posture, sense of, 339–342
Pressure gradient, 319
Pretori, H., 83, 174
Primary colors, additive, 159–163
  psychological, 140, 142, 144, 170, 171, 173, 355
Prism, olfactory, 360–361
Propagation, in nerve, mechanism of, 24–26, 28–29
Proprioceptors, 13–14
  musculoskeletal, 337–338
Protanopia, 196, 199
Puitti, A., 281
Pupil, area, as function of intensity, 111
  of eye, 100, 110–111
Purdy, D. McL., 149, 167, 168, 170–171
Purity, chromatic, 356
  of visual stimulus, 61–62
Purkinje, J., 91
Purkinje phenomenon, 70–71, 119, 179, 217
Purples, series of, 147

Q

Quality, 2
  general basis of, 349
Quanta, in nerve action, 17, 18, 37

R

Radiant energy, characteristics of, 58–60
  heterogeneous, 58–59
  homogeneous, 58
Radiant sources, distribution curves of, 63–64
Radiometry, 62
Ramsay, W., 264
Rays, on stars, 107
Reaction time, tactual, 316

Reaction time, thermal, 304–305
Reaction times, gustatory, 287
Receptor cell, mechanism of, 41–45
Receptor process, 1, 8, 11–12
  phasic, 43
  postural, 43
  tactual, 318–320
  visual, 43–45
Receptors, contact, 14
  distance, 14
  gustatory, mechanism of, 289–295
  olfactory, 275
  tactual, 318
Reciprocity law, in vision, 122–123
Recovery, chromatic, 181
  retinal, 94
Reeves, P., 111
Reflection, laws of, 64–66
Reflex arc, properties of, 45
Refractory phase, in nerve, 30–33, 38–39, 50
Regeneration, of nerve fibre, 297–298
Resolving power, retinal, 133–134
Retina, "inverted," 104
  structure of, 101
Retinal illumination, 63, 110
Rhodopsin, 118, 120, 189, 197
Rich, G. J., 223, 224
Richet, Ch., 284
Rivalry, olfactory, 272, 273
  retinal, 203–204
Rivers, W. H. R., 344
Rod cells, of retina, 101–104
Rods, retinal, 101–104, 117, 188
Ruffini, 307, 345
Ruffini's corpuscles, 308
  papillary endings, 308
Rutherford, W., 244

S

Saccharin, 281
Sacculus, 330, 331–333, 334
Sachs, M., 174
Saito, Y., 343
Saltiness, 281–282, 292–293, 362
Salzer, F., 105
Saturation, 54, 139, 156, 353
  as function of intensity, 167–169
  as function of purity, 148
  as function of wave-length, 147–149
  intraocular influences on, 183–184
  maximal, 168–169
  scale, 148
Scala vestibuli, 242
Scattered light, in eye, 112, 184
Schirmer, R., 287
Schjelderup, H. K., 79, 112
Schreiber, C., 286
Schriever, H., 315
Sclerotic coat, of eye, 98
Scotopic vision, 70
Secondary process, in retina, 127–128
Semicircular canals, 330–331
Sensation, 2
  and afferent arc, 4
  and the cerebrum, 4
  auditory, 206, 260, 357–359
  auditory, introspective analysis of, 357–359
  component, 6
  composite, 6
  concept of, 1–50
  cutaneous, 362–365
  definition of, 1–3, 7
  departments of, 13–14
  general nature of, 1–8
  generalizations concerning, 349, 350
  internal, 347–348, 365–370
  James on, 3
  kinaesthetic, 329–348
  muscular, 344
  olfactory, 261–280
  organic patterns of, 370
  science of, 7
  spatial determinants of, 350
  temporal determinants of, 350
  temporal variations of, 6
  temporally conditioned, 6
  thermal, 299–300, 363
  Titchener on, 2
  visual, 51–205, 351–356
Sensationalism, 8
Sense-organ, auditory, psychophysiological relationships of, 240–260
  process, 8, 11
  visual, 97
Sensibility, deep, 344
Sensitivity, for brilliance, 93–95
Sensory circle, 321
Sherrington, C. S., 13, 45, 50, 204, 324, 336, 345
Schultze, M., 117
Sinden, R. H., 154, 166, 167, 185–186

Skin, receptors of, 306
Smell, sense of, 261–280
Smith, F. O., 147
Snake figure, 114
Sommer, G., 303
Sound, 207
Sourness, 282, 292–293, 362
Space, auditory, 358
Spatial configurations, tactual, 321–322
Specific brightness, of colors, 198
Spectrum, 59, 61
Speech, 236, 239–240
Stapes, 242
Steindler, O., 142
Stiles, P., 338
Stimulus, 8
  absolute kinaesthetic, 329
  auditory, 206–209
  genetl nature of, 9–10
  gustatory, 280–281
  olfactory, 262–263
  pain, 324
  reacting, 95, 180
  relative proprioceptive, 337–338
  tactual, 312–313, 318
Stretch reflex, 344, 345, 346
Structures, sensory, 5
Strughold, H., 307, 325
Strümpell, A., 340
Stumpf, C., 228, 229
Sugars, 293
Sulzer, D., 89, 177
Summation, neural, 49
Summation tones, 232–233, 247, 252
Sweetness, 281, 293, 362
Synapses, processes of, 47–50
  properties of, 45–47

T

Tactual experience, neurological relations of, 321–323
Tactual intensity, as function of stimulus, 313, 314, 315, 316
Tactual quality, as function of stimulus, 313, 314
  as function of time, 316
Tactual sensation, 312–323
  composite, 317, 318
  introspective analysis of, 362–363
Tactual stimulus, 312–313
Talbot-Plateau law, 92–93, 123, 178
Tanzi, E., 305
Taste, alkaline, 283
  introspective analysis of, 362
  sense of, 280–295
Taste-buds, 286, 290–292
  distribution of, 291
  specific energy of, 291
  metallic, 283
Temporal patterns, tactual, 322, 323
Tendons, 338, 346
Tensive experience, 342
Tensive qualities, 346
Ter Kuile, E., 244
Thermal experience, as a function of temperature, 301
  as function of time, 304–306
  neurological correlations of, 311–312
Thermal sensation, 299–312
Thermal sense, Weber's theory of, 300
Thermal sensibility, end bulbs for, 306, 307, 308
  hypothesis of, 308–311
Thirst, 366, 367
Three-color mixture principle, 156
Three-color theory, 188–189
Three-component theory, 188–197
Threshold, chromatic time, 177
  mechanism of, in nerve, 24–26, 28
  pain, 325
  relative acoustic frequency, 221
  relative, for brightness, 78–79
  tensive, 342
Thresholds, articular kinaesthetic, 341
  auditory, 211
  gustatory, 284
  kinaesthetic, 341
  olfactory, 266–267
  thermal, 301, 302, 304
Thunberg, J., 323
Tickle, stimulus for, 313–314, 316, 320
Tigerstedt, R., 318
Timbre, 234, 359
Titchener, E., 2, 14, 139, 239, 290, 292, 315, 332, 336, 337, 339, 344, 356, 359
Tonal manifold, coördinates of, 358
Tones, attributes of, 357–358
  combinational, 231
  difference, 232
  intermediate, 231–232
  summation, 232–233
Touch, 363

Touch spots, distribution of, 315, 316
Transmission, laws of, 64–66
Triangle, color-mixture, 156–163, 184
Trichromatism, anomalous, 197
Tritanopia, 196
Trotter, W., 298
Two-point limen, tactual, 317, 321
Tympanum, 240, 241, 245
Tyndall, J. B., 265

U

Ultra-violet rays, 61
  visibility of, 110
Unit area, chromatic, 190, 191
  visual, 134–136
Urbantschisch, V., 238
Utriculus, 330, 331–333, 334

V

Van t'Hoff's law, 309
Varess, E., 262
Vertical, kinaesthetic, 334, 365
Vertigo, 335, 365
Vibration sense, 316, 323
Violet, 192
Visibility, absolute, 72
  curve, retinal, 108–109, 119, 191
  curves, 68–70, 73, 119
  function, 72
  values, 69–70
Vision, photopic, 78
  scotopic, 78, 118
Visual acuity, 85–87
  Hecht's theory of, 133–136
Visual changes, 53
Visual patterns, 52–53
Visual purple, 118, 189
Visual sensation, 51–205
  binocular, 52, 55
  monocular, 52
  problems of, 51–53
Visual stimulus, nature of, 55–66
Visual theory, problem of, 116–117
Vocables, 357
  basillary basis of, 253
  neural foundations of, 258
  sensory correlations of, 226–229
Vocalic quality, 359
Vocality, 359
Voeste, H., 171, 180
Voltalini, 244
Volume, auditory, 224, 358
  basillary relations of, 249
  neural foundation of, 259–260
Von Frey, M., 298, 303, 308, 313, 314, 317, 318, 323, 324, 343
Von Kries, J., 91, 94
Vowels, 226–228, 357

W

Waller, A. D., 29, 244
Warm spots, 303
Warmth, receptor process for, 309
  receptors, 308, 309, 310
Wave-front, auditory, neural, 259
Wave-length discrimination, visual, 142–147
Wave-length, measures of, 60–61
  of radiant energy, 58, 60–62
Weber, E. H., 262, 300, 305, 314, 315, 325
Weber function, for pitch, 219–222
Weber's law, for brilliance, 76–80
  for pain, 325
  for tension, 342
  in audition, 214–216
  in thermal experience, 302
Wegel, R. M., 217, 232, 233, 244, 248, 250, 251
Weinberg, M., 237, 288, 289
Westphal, H., 142
"White light," 66
Wien, M., 213
Williams, H. B., 347
Winter, J. E., 339, 340, 341
Wright, W. D., 159
Wundt, W., 226

X

X-rays, 61

Y

Yellow, 20, 177, 192
Yellow-spot, of retina, 105, 114, 185
Young-Helmholtz, color theory, 188, 189–197

Z

Zero, physiological, 299, 305
Zotterman, Y., 41, 318, 347
Zuntz, N., 288
Zwaardemaker, H., 262, 266, 267, 270, 273, 274, 279, 360

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